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DESCRIPTION OF NESTS, EGGS, AND NESTLINGS OF THE ENDANGERED NIGHTINGALE REED-WARBLER ON SAIPAN, MICRONESIA

STEPHEN M. MOSHER[1,2,3,5] AND STEVEN G. FANCY[1,4]

ABSTRACT.—We describe the first verified nests, eggs, and nestlings of the Nightingale Reed-Warbler (*Acrocephalus luscinia*), an endangered species endemic to the Mariana Islands, Micronesia. Nest composition, nest dimensions, and eggs were studied on the island of Saipan. Nests were located within three habitat types: upland introduced tangantangan (*Leucaena leucocephala*) forest, a native mangrove (*Bruguiera gymnorrhiza*) wetland, and a native reed (*Phragmites karka*) wetland. Nesting substrates included five native and two introduced tree species and one native reed species. Nests were composed primarily of dry vine stems, needle-like branchlets of ironwood (*Casuarina equisetifolia*), and tangantangan petioles. Nests were compact to bulky in construction and were secured to a forked arrangement of branches or stems. The background color of eggs ranged from white to cream to ivory-buff. Eggs were spotted, speckled, and blotched with gray, brown, black, and rust colored markings. Clutch size was 2–4, with a mode of two. Hatchlings were altricial with closed eyelids and devoid of natal down with dark gray to black skin. Nestlings examined prior to fledging resembled the adult plumage, except for the lack of the yellow supercilium found in adults. The nests and eggs have some characteristics similar to those of other Acrocephaline warblers found throughout Micronesia and Polynesia. *Received 29 September 2000, accepted 18 March 2002.*

The breeding biology of most endemic passerines in the Northern Mariana Islands is poorly known and the Nightingale Reed-Warbler (*Acrocephalus luscinia luscinia*) on the island of Saipan is no exception. The lack of reproductive information about the Nightingale Reed-Warbler hinders the development of management practices for conserving this species on Saipan. The reasons for this lack of vital life history information is, in part, due to relatively few field investigations going beyond presence/absence surveys of bird species in the Northern Mariana Islands. Some exceptions to this were Craig (1989, 1990, 1992), who studied the foraging ecology of Bridled White-eyes (*Zosterops conspicillatus*) and Golden White-eyes (*Cleptornis marchei*), as

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FRONTISPIECE. Nightingale Reed-Warbler (*Acrocephalus luscinia*) nestlings at 14 days of age on the island of Saipan, Northern Mariana Islands, 11 February 1998. Nest constructed of dry exotic vine species and placed in introduced *Leucaena leucocephala*. Photograph by SMM.

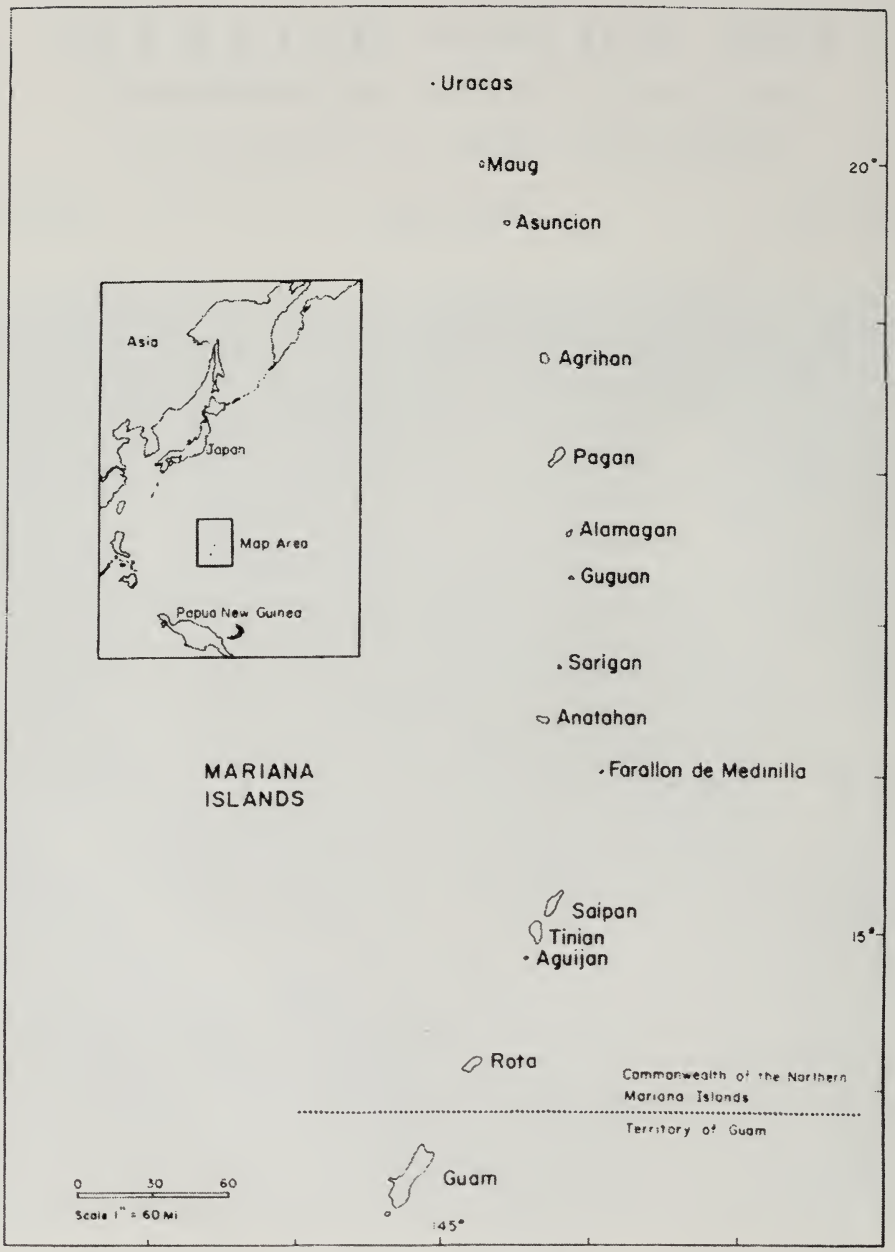

FIG. 1. Map of the Mariana Islands.

well as territoriality and habitat use of Nightingale Reed-Warblers, and Stinson and Stinson (1994), who studied breeding ecology of Golden White-eyes. Of the 16 native forest bird species found in the Mariana Islands archipelago, only five have been subjects of natural history or ecological investigations (Rodda et al. 1998).

The Nightingale Reed-Warbler is a long-billed, Old World warbler currently found on the islands of Saipan, Alamagan, and Aguijan within the Marianas archipelago (Pratt et al. 1987, U.S. Fish and Wildlife Service 1998; Fig. 1). The reed-warbler has become extinct on the islands of Guam and Pagan during the latter half of the Twentieth Century (Reichel

et al. 1992) and prehistorically on the island of Tinian (Steadman 1999). The current population estimate for Nightingale Reed-Warblers in the Mariana Islands is approximately 4,572–4,577 individuals: 1–6 on Aguijan, 346 on Alamagan, and 4,225 on Saipan (U.S. Fish and Wildlife Service 1998, Commonwealth of the Northern Mariana Islands–Div. of Fish and Wildlife 2000). At this time there is no information on the breeding ecology of reed-warblers on Alamagan and Aguijan. Here we present the first detailed description of Nightingale Reed-Warbler nest structure and composition, and the first recorded descriptions of eggs and nestlings for this species. We also include additional information on nest substrate and placement.

STUDY AREA AND METHODS

Saipan (15° 10′ N, 145° 45′ E) is located in the central region of the 15-island Mariana archipelago. The Marianas form a north-south chain of islands about midway between Japan and New Guinea in the western Pacific. Saipan is the second largest island in the Marianas with a land area of 123 km². The island is of limestone and volcanic origin approximately 22 km long and 6 km wide (Fig. 1), with a maximum elevation of 474 m. The climate is tropical with an annual mean temperature of 28.3° C. The humidity is high with monthly means between 79 and 86%. Mean annual rainfall is about 213 cm. Saipan has a dry season from December to June and a wet season from July to November (Young 1989). Typhoons can occur during any month, but are most frequent from August to December, with a mean of one typhoon per year affecting the Mariana Islands (Young 1989, Mueller-Dombois and Fosberg 1998).

This study focused on three habitat types utilized by reed-warblers: upland introduced tangantangan (*Leucaena leucocephala*) complexes, a tall native reed (*Phragmites karka*) wetland, and a native mangrove (*Bruguiera gymnorrhiza*) wetland. Upland tangantangan habitats were dominated by monotypic stands of tangantangan with no understory, as well as tangantangan/sword grass (*Miscanthus floridulus*) and/or elephant grass (*Pennisetum purpureum*) mosaics. Some stands of tangantangan had a dense understory of introduced lantana (*Lantana camara*) and others had scattered native shrubs. The tall reed wetland consisted of a dense monotypic stand of *Phragmites* with a mosaic of native and introduced tree and shrub species surrounding the wetland. The mangrove wetland consisted of small stands of mangroves, dense thickets of sea-hibiscus (*Hibiscus tiliaceus*) and rosewood (*Thespesia populnea*), scattered stands of tall ironwood trees (*Casuarina equisetifolia*), and other native and introduced tree and shrub species. The amount of understory vegetation varied throughout the mangrove wetland.

We conducted research between mid-January 1997 and mid-July 1998 in the Marpi region, Naftan Peninsula, Chalan Lao Lao region, and American Memorial Park. Nest searching was conducted by active searches of known reed-warbler territories throughout the year and with the aid of radio marked birds at the initiation of the study. Nests were examined and measured after fledging or failure to obtain detailed descriptions. Eggs were measured and weighed using electronic calipers and a Pesola scale. Nestling descriptions were obtained by viewing into the nest with a mirror pole and binoculars and during the banding of nestlings prior to fledging. We recorded measurements of mass, unflattened wing chord, exposed culmen, culmen, tail length, and tail feather count for nestlings prior to fledging.

RESULTS

Nesting behavior.—A total of 100 reed-warbler nests were located on Saipan between mid-January 1997 and mid-July 1998. We located 84 nests in upland introduced tangantangan forest, 15 in a native mangrove wetland complex and one in a native reed wetland. Fifty-one of these nests were active when found (four during building, 12 prior to egg laying, 26 during incubation, and nine during brooding). We found no reed-warblers nesting in native limestone forest even when their territories included limestone forest fragments or were adjacent to limestone forest. Reed-warblers that inhabited the reed wetland were not found to nest outside of the reed bed in the wooded area surrounding the wetland. We observed reed-warblers carrying nesting material into the reed wetland on several occasions. Juvenile reed-warblers were heard making begging calls within the dense reeds, but no active nests were located.

Two peak nesting periods were observed during the study, one from January through March and the other from July through September. Active nests were located during all months, except November and December. Twenty-seven of the active nests were located during January through March (dry season) and 20 during July through September (wet season). This study covered two dry season nesting periods and one wet season nesting period. Reed-warblers had a principal nesting area within a given territory, where several nests from previous nesting attempts sometimes were found in close proximity to one another. Locating the principal nesting area of

TABLE 1. Materials used in Nightingale Reed-Warbler (*Acrocephalus luscinia*) nests in two habitats on Saipan, 1997–1998. Values are number of nests (%) in which the listed material occurred.

	Upland tangantangan (n = 67 nests)		Mangrove wetland (n = 9 nests)	
Material	Outer	Lining	Outer	Lining
Vines[a]	67 (100)	4 (6)	9 (100)	0 (0)
Dry grass blades[b]	15 (22)	1 (1)	1 (11)	0 (0)
Dry bark strips[c]	15 (22)	0 (0)	1 (11)	0 (0)
Spider web casings	7 (10)	0 (0)	0 (0)	0 (0)
Petioles[c]	4 (6)	66 (99)	0 (0)	2 (22)
Branchlets[d]	3 (4)	8 (12)	8 (89)	9 (100)
Twig[c]	1 (1)	0 (0)	0 (0)	0 (0)
Leaf	1 (1)	0 (0)	0 (0)	0 (0)

[a] *Momordica charantia* and/or *Passiflora foetida*.
[b] *Pennisetum purpureum* and/or unknown spp.
[c] *Leucaena leucocephala*.
[d] *Casuarina equisetifolia*.

a reed-warbler pair facilitated future search efforts.

Females gathered nesting material and constructed the nest while the male sang from a nearby perch. On a few occasions we observed males carrying nesting material to the nest, whereupon the female received and placed the material. One male was observed attempting to place nesting material into the nest, but upon unsuccessful placement returned to singing from an adjacent perch. We observed two nests that were constructed directly on top of old deteriorating nest material. On three occasions nests in the beginning stages of construction were dismantled and reconstructed with the same nesting material in a nearby tree. We never observed a nest used more then once.

Nest composition.—We examined 73 nests to determine the composition of the outer nest structure and cup lining, including nests from upland tangantangan forest (n = 67), a mangrove wetland (n = 9), and a reed wetland (n = 1). Table 1 summarizes the nesting material found in nests from upland tangantangan forest and a mangrove wetland forest. Dry vine stems and tendrils of introduced bitter melon (*Momordica charantia*) and wild passionfruit (*Passiflora foetida*) consistently were the primary component used to form the outer structure. The only exception to this was a nest found in the mangrove wetland, which was constructed entirely of ironwood branchlets. The cup lining of nests found in upland tangantangan forest were almost exclusively composed of tangantangan petioles, while nests in the mangrove wetland had a larger amount of ironwood branchlets incorporated into the cup lining. Ironwood branchlets were incorporated into the nest structure when ironwood trees were located near the nest site. The one nest found in the native reed wetland had an outer structure of dry vines, dry coarse reed blades, and one spider web casing, and a cup lined with reed panicles.

Nest structure.—Nests were of two forms: (1) tightly woven compact nests, or (2) larger tightly woven nests with bulky outer material. Nests had open cups that were circular to ovoid in shape. In some nests the inner rim was tightly woven to form an overhanging lip, which may aid in keeping eggs in the nest during high winds. We measured 66 nests from among the three habitat types studied. Outer nest diameter was 106 mm ± 10, 83–127 mm (mean ± SD, range), and height was 90 mm ± 20, 57–177 mm. Cup diameter was 65 mm ± 6, 46–86 mm, and cup depth was 45 mm ± 7, 29–58 mm. Rim width at the lip was 20 mm ± 4, 12–28 mm, and rim width at base of the cup was 28 mm ± 6, 17–48 mm. The nest found in the native reed wetland was a loose compact nest with an outer diameter of 117 mm, height of 98 mm, cup diameter of 56.5 mm, cup depth of 43 mm, rim width at lip of 25 mm, and a rim width at base of 32 mm.

Nest placement.—Reed-warblers used seven tree species as nesting substrates. In upland habitat 79 (94%) of the nests were found in introduced tangantangan trees, four (5%) in native lipstick trees (*Ochrosia mariannensis*), and one (1%) in an introduced madras thorn tree (*Pithecellobium dulce*). We found 15 nests in the mangrove wetland forest including six (40%) in native ironwood trees, four (27%) in native sea-hibiscus, three (20%) in mangrove, one (7%) in rosewood, and one in madras thorn. The nest found in the reed wetland was attached to reed stems. Vegetative cover above, below, and around nests varied among substrates.

Nest placement within tangantangan consisted of nests being attached to the main stem/trunk and several lateral branches with at least one branch supporting the bottom of

FIG. 2. Placement and structure of Nightingale Reed-Warbler (*Acrocephalus luscinia*) nests, Saipan, February 1997 to July 1998. (A) Typical nest placement within introduced *Leucaena leucocephala*. (B) Typhoon-damaged *Leucaena leucocephala* trunk with lateral placement of the nest. (C) Nest placement in fork of native *Ochrosia mariannensis*. (D) Nest attached to drooping branch of indigenous *Casuarina equisetifolia*. Photographs by SMM.

the nest (Fig. 2a). Some nests located in tangantangan were constructed on the top of typhoon-damaged trunks supported by regrowth branchlets (Fig. 2b). Nests found in native lipstick trees were supported by the main trunk and 3–5 branches that forked from the center of the tree (Fig. 2c). Four of six nests in ironwood trees were attached to high drooping branches that extended away from the main trunk (Fig. 2d). The one exception to the above placement types was a nest located at the terminal end of a lateral branch of a mangrove tree. The nest found in the reed wetland was supported by three vertical reed stems and

two leaning stems, which supported the bottom of the nest.

Nests were securely attached to support branches/stems with vines either looping around supports or weaving around the support and concealing the support branch/stem within the structure of the nest. In all substrates used for nesting, there always was a branch or stem supporting the base of the nest.

We measured 83 nest trees. Mean nest height was 4.3 m ± 1.3, 2.3–10.0 m and nest tree height was 6.1 m ± 3.4, 3.4–25.0 m. Diameter (dbh) of nest trees was 60.7 mm ± 59.7, 17.7–318.3 mm. Mean number of support branches for 76 nest trees was 3.9 ± 1.2, 2–8 with a mode of four. Diameter of support branches, including the main stem, was 8.0 mm ± 4.6, 1.8–30.5 (n = 282 supports). The nest found in the reed wetland was 2.2 m high and 0.8 m below the tops of the reeds.

Eggs.—Eggs were subelliptical and varied from dull white to cream to ivory-buff. Eggs were spotted, speckled, and blotched with irregularly shaped markings usually well distributed over the entire shell, commonly with a heavier zone of overlapping markings around the broader end. Markings were gray, brown, black, and rust in color, and ranged in size from pinpoints to one that was 2.3 mm in diameter (Fig. 3). The depth of the markings was variable within the cuticle. Egg surface was smooth and nonglossy, with a slightly granular appearance. Mean egg length (n = 50) was 23 mm ± 1.2, 21.0–25.8 mm and width was 16.9 mm ± 0.5, 15.9–18.0 mm. Mean egg mass (n = 49, age unknown) was 3.1 g ± 0.5, 2–3.8 g. Clutch size was 2.5 ± 0.7, 2–4, with a mode of 2 (n = 20 nests).

Nestlings.—Nestlings hatched with closed eyelids, dark gray to black skin, and totally devoid of natal down, with bright yellow gape flanges. Prior to fledging, nestlings (n = 43) were almost completely feathered, except around the eyes, ears, chin, and throat (Fig. 4). Plumage was brown on all dorsal surfaces with thin buff edges around primaries, secondaries, and on the tips of the rectrices. The breast, belly, vent, thighs, and undertail coverts were light yellow to cream, with the flanks brownish yellow to buff. The maxilla was grayish black with broad yellow edges, while the lower mandible was fleshy pink with broad yellow edges. Three rictal bristles were visible on each side of the mouth above the gape flanges. The palate was reddish pink and the tongue yellow with two oblong brown

FIG. 3. Nightingale Reed-Warbler (*Acrocephalus luscinia*) eggs, Saipan, 1998. Photograph by SMM.

FIG. 4. Nightingale Reed-Warbler (*Acrocephalus luscinia*) nestling at day 12, Saipan, 7 October 1997. Photograph by SMM.

spots just below the tongue spurs. Legs and toes were grayish blue and foot pads yellowish, with strong well-developed claws black above and yellowish below. The iris was brownish. The egg tooth was still present on the tip of the bill 2–3 days prior to fledging. Nestlings lacked the pale yellow supercilium and black lores present in the adult plumage.

We measured 42 nestlings prior to fledging at an age of approximately 14 ± 2 days. Mean mass of nestlings was 28.4 g ± 2.7, 24–35 g, wing chord was 50.3 mm ± 4.9, 39–58 mm, exposed culmen was 17.7 mm ± 1.7, 15.1–22.9 mm, culmen was 10.4 mm ± 0.9, 8.4–11.6 mm, and tail length was 13.3 mm ± 4.0, 4.0–20.5 mm. The mean number of tail feathers for 41 nestlings was 10.2 ± 0.8, 9–12, with a mode of 10.

DISCUSSION

Prior nest descriptions.—M. Alfred Marche found the first presumed Nightingale Reed-Warbler nest in June 1887 in a wetland on Guam (Oustalet 1895). It was a laterally compressed oval cup, with a height of 50 mm and an outer diameter of 120 mm, and was constructed of rush stems and grass blades roughly woven together. There was no mention of how the nest was determined to be that of a reed-warbler. The nest was found in a wetland, likely a native reed wetland where reed-warblers commonly were found by early observers on Guam (Baker 1951, Reichel et al. 1992). Oustalet's nest measurements were similar to the one nest found during this study in a reed wetland on Saipan. Our Saipan nest was similar in width to his Guam nest, but was 48 mm taller. There was no mention by Oustalet of how the nest was placed and secured. The difference in nesting material found in the Guam nest, rush stems and grass blades verses predominately dry vine stems with some reed blades in the Saipan nest, may reflect differences in the availability or selection of nesting materials between the birds once found on Guam and the ones presently on Saipan.

Engbring et al. (1986) described a nest they found in 1982 as a large bulky nest of grasses. The nest was located in the fork of a tangantangan tree 6 m above the ground. The nest was not collected because of the presence of a young fledgling begging near the nest. The nest found by Engbring et al. (1986) fits the nest placement profile of a reed-warbler nest in upland tangantangan forest, but their description that the nest was composed of grasses does not follow the findings of this study. It is possible the nest was composed primarily

of vines that were mistakenly identified as grasses.

R. J. Craig (unpubl. data) found an empty nest in 1988 within a known reed-warbler territory, approximately 4 m above the ground in a 4.6-m tangantangan tree. In a drawing by Craig (unpubl. data), the nest appears to be attached to upper canopy branches with at least three small diameter support branchlets. Craig's drawing of the nest depicts the same structure, placement, and attachment in the fork of a tangantangan tree, as was found in this study. Craig mentioned that the nest was constructed of fine and coarse material with strands of fibers hanging below the nest, a depiction resembling the appearance of a nest composed of dry vine stems. He estimated the nest was 150 mm in height with an outer diameter of 150 mm. His height estimate was within the range of variation we found among the nests we measured, but the outer nest diameter was about 23 mm wider than the largest nest we found.

Nesting behavior.—We found reed-warblers nested primarily from January through March and again from July through September. This is consistent with prior observations of territorial behavior (Craig 1992). Male reed-warblers are highly territorial and defend territories by singing (Craig 1992). Craig (1992) observed an increase in occupied territories during January through February and during May with a subsequent decline in territory occupancy by September, which he attributed to a decline in breeding activity. Furthermore, surveys conducted by Craig (1996) during January and July of 1991 and 1992 revealed an increase in the number of singing males during those months.

The small number of nests found in wetland habitats compared to upland tangantangan habitat probably does not reflect low densities of reed-warblers, but rather the relative difficulty in locating reed-warblers and their nests in dense wetland vegetation. Close proximity of several nests from a breeding pair's separate attempts also has been observed in other Pacific reed-warblers: *Acrocephalus syrinx* of the Caroline Islands (Finsch 1881), *A. aequinoctialis* of the Line Islands (Schreiber 1979) and *A. taiti* of Henderson Island (Graves 1992). Construction of the nest by the female with little or no help from the male also has been observed in the Tahitian Reed-Warbler (*A. caffer*), Tuamotu Reed-Warbler (*A. atyphus*), and the Marquesan Reed-Warbler (*A. mendanae*; Bruner 1974), as well as the European Reed-Warbler (*A. scirpaceus*; Brown and Davies 1949). Building and dismantling newly constructed nests and then rebuilding them with the same material in a different location has been observed frequently in the European Reed-Warbler (Brown and Davies 1949).

Nest composition.—Of the other reed-warblers recognized in the Pacific, only the Line Island Reed-Warbler, Tahitian Reed-Warbler, Marquesan Reed-Warbler, and Tuamotu Reed-Warbler are known to use vines in the outer nest structure (Tristram 1883, Holyoak 1973, Bruner 1974). Coconut fibers and grasses are the most common nesting materials documented among eight of the 11 other Pacific Island reed-warblers (Tristram 1883, Hartert 1900, Kirby 1925, Yamashina 1932, Gallagher 1960, Williams 1960, Brandt 1962, Holyoak 1973, Bruner 1974, Schreiber 1979, Graves 1992, Brooke and Hartley 1995, Buden 1996, Morin et al. 1997). Pacific Island reed-warblers appear to be generalists in their selection of nesting materials, using the most common materials available within their respective habitats.

The Nightingale Reed-Warbler also is opportunistic in its use of nesting materials. Dry stems of bitter gourd and wild passionfruit constituted the bulk of nesting material found in most nests. These two plant species were common ground and understory flora within the three habitat types studied. Neither species of vine is native to the Mariana Islands, with bitter gourd native to tropical or subtropical Asia and Africa and wild passionfruit native to tropical America (Whistler 1994).

The reed *Phragmites karka* is found in fresh and brackish water marshes and is indigenous to the Mariana Islands and the western Pacific (Stemmermann 1981). The only nest that contained a large amount of grass blades and panicles incorporated into the nest body and cup lining was the nest located in the reed wetland where these two components were abundant. Brown and Davies (1949) found that European Reed-Warbler used dry *Phragmites* panicles almost exclusively for lining nest cups

and to a lesser degree in the outer nest structure.

The use of spider webs for securing nests to substrates, as well as for binding nesting materials together is found in a number of species within the families Tryannidae and Muscicapidae (Baicich and Harrison 1997). However, the function of spider web casings in the outer structure of Nightingale Reed-Warbler nests is unclear, as they did not appear to aid in binding nesting material together or in securing the nest to the substrate.

Eggs and nestlings.—The nest found on Guam by Marche in 1887 contained three eggs, but they were not described because they were rotten upon reaching their final destination (Oustalet 1895). The three-egg clutch in Marche's nest was within the range found on Saipan during this study (2–4). The clutch size of the Nightingale Reed-Warbler falls in the middle among Pacific Island reed-warblers with one egg in the Cook Islands Reed-Warbler (*A. kerearako*) and up to five in the Henderson Island and Marquesan reed-warblers (Bruner 1974, Holyoak 1980, Brooke and Hartley 1995).

The background color of Nightingale Reed-Warbler eggs was consistently dull white to ivory buff, whereas most other Pacific Island reed-warbler eggs range from pale blue to olive. Spots, speckles, and blotches (usually brown or black) are found on eggs of all Pacific Island reed-warblers (Tristram 1883, Hartert 1900, Yamashina 1932, Williams 1960, Brandt 1962, Pearson 1962, Bruner 1974, Schreiber 1979, Holyoak 1980, Brooke and Hartley 1995, Morin et al. 1997).

Nestlings prior to fledging (2–3 days) had similar plumage characteristics as adults on most dorsal (brownish) and ventral (yellowish) surfaces (Baker 1951). Plumage around the eye was one of the last tracts to be feathered. This resulted in a lack of the adult's pale yellow supercilium and black lores among fledglings. Most passerines have 12 tail feathers (Gill 1995), but the significance of the variation in the number of tail feathers of Nightingale Reed-Warbler nestlings, nine to 12 with a mode of 10, is not understood.

Additional information collected on Nightingale Reed-Warbler nesting behavior and success, as well as nest site selections, will be the focus of future publications. Ecological investigations into the breeding biology on the island of Alamagan in the Mariana Islands would be another important step toward the future recovery of this species.

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THE CHANGING STATUS OF MARINE BIRDS BREEDING AT SAN BENEDICTO ISLAND, MEXICO

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ABSTRACT.—We reviewed the status of the breeding marine birds on San Benedicto Island, Mexico, based on >100 years of published observations and seven of our own surveys conducted between 1978 and 2000. We found that there have been marked changes in the island avifauna with two main trends evident. First, a volcanic eruption destroyed much of the island in 1952. The Wedge-tailed Shearwater (*Puffinus pacificus*; estimated breeding population 1,000 pairs), Townsend's Shearwater (*Puffinus auricularis*; probable breeder, small numbers), and Red-footed Booby (*Sula sula*; 60 pairs) historically had much larger populations, but they apparently never fully recovered from the eruption. The Masked Booby (*Sula dactylatra*; 2,185 pairs), however, has become much more abundant perhaps due to changes in the vegetation. The second trend is that within the last three decades at least two, and possibly four, species from the central Pacific have colonized the island. The Laysan Albatross (*Phoebastria immutabilis*; 12 pairs) started breeding in the late 1980s; Black-footed Albatross (*Phoebastria nigripes*; 1 pair) in 2000. Red-tailed Tropicbirds (*Phaethon rubricauda*; probable breeder, 10 pairs) may have started breeding in the 1980s, and at least some of the breeding Brown Boobies (*Sula leucogaster*; 300 pairs) are from central Pacific populations. The reason(s) for this influx of central Pacific species is unknown, but likely involves changes in the marine environment. Other breeding species include the Red-billed Tropicbird (*Phaethon aethereus*; 200 pairs), Nazca Booby (*Sula granti*; 50 pairs), Great Frigatebird (*Fregata minor*; 165 pairs), and Magnificent Frigatebird (*Fregata magnificens*; 5 pairs). *Received 21 June 2001, accepted 16 April 2002.*

The Revillagigedo Islands are comprised of four scattered volcanic islands off the Pacific coast of Mexico: Socorro, San Benedicto, Clarión, and Roca Partida. San Benedicto Island (19° 18′ N, 110° 49′ W) is located 370 km south of the tip of Baja California. It is a small (6.4 km × 3.2 km), uninhabited, oceanic island. In August 1952, it erupted and formed a new volcanic crater (Bárcena) next to the old one (Herrera; Fig. 1). The eruption eliminated all of the terrestrial plant life, destroyed most of the nesting seabirds, and drove to extinction the only resident landbirds: Common Raven (*Corvus corax*) and an endemic subspecies of Rock Wren (*Salpinctes obsoletus exsul*; Townsend 1890, Brattstrom 1963). By November 1953 the biological recovery of the island was underway; vegetation was sprouting and seabirds were roosting and starting to nest again.

Ornithological investigations of the island occurred during three distinct periods (Table 1). Early expeditions established a bird list for the island but provided only qualitative assessments of the number of birds present (Townsend 1890; Anthony 1898, 1900; Kaeding 1905; Hanna 1926; McLellan 1926). Interest in documenting the fate of the island biota in the aftermath of the eruption stimulated a second period of investigation (Brattstrom and Howell 1956, Brattstrom 1963). After another hiatus of about 25 years, the recent era of renewed interest began (Jehl and Parkes 1982, Brattstrom 1990, Howell and Webb 1990, Howell and Webb 1992a, this study).

In this paper we review the history and update the current status of marine birds breeding at San Benedicto Island, and discuss the major changes that have occurred there over time. An appendix lists landbird vagrants we recorded on the island.

STUDY AREA AND METHODS

The southern half of San Benedicto formed when Bárcena volcano erupted in 1952; it is still covered with thick ash and supports almost no vegetation and few nesting birds. Our surveys on land were limited almost entirely to the northern half of the island which is vegetated mainly with dense patches of bunch grass (*Eragrostis diversiflora*). Richards and Brattstrom (1959) presented a physical description of the island, and Levin and Moran (1989) described the flora.

We visited the island seven times between 1978 and 2000, conducting surveys that typically lasted several hours on a single day (Table 1). In order to census the Masked Booby (*Sula dactylatra*) population, on four of our visits we photographed the entire island with a

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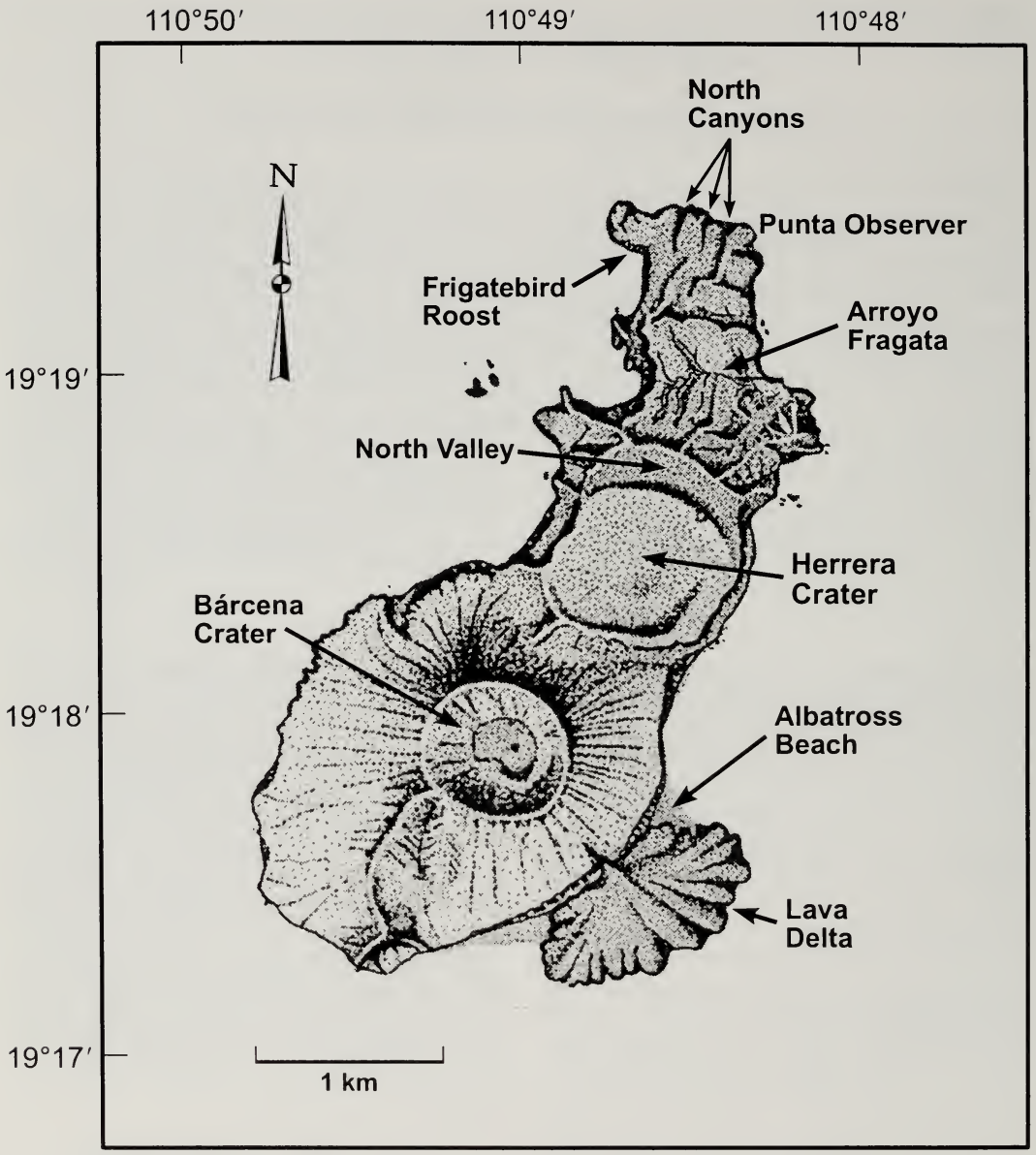

FIG. 1. San Benedicto Island, Mexico (after Richards and Brattstrom 1959).

series of overlapping images taken from a helicopter equipped with a large format (126 mm), belly-mounted camera. All aerial photographs will be permanently archived with the Map and Imagery Laboratory at the Univ. of California at Santa Barbara. For our historical review, in addition to published accounts, we also reviewed the field notes of E. Harrison (on file at Western Foundation of Vertebrate Zoology), who visited the island on 16 March 1938 and 20 April 1940, and S. N. G. Howell (unpubl. data), who visited the island on 25 April 1992.

RESULTS AND DISCUSSION

We observed a total of 13 species of marine birds at San Benedicto Island; nine are confirmed breeders, three are probable breeders, and one a possible breeder.

Species accounts.—Laysan Albatross (*Phoebastria immutabilis*). We first observed this winter breeder roosting on the island in May 1987. Although we first found it breed-

ing in November 1990, it could have bred during any of the three previous seasons. Nearly all of the nesting occurs on the upper part of the island, along the north and west rim of Herrera Crater, and along the ridge running east-west just north of the crater. In 2000, one pair nested on Albatross Beach for the first time (Fig. 1). Although the population at San Benedicto is still small, it appears to be increasing steadily (Table 1).

Black-footed Albatross (*P. nigripes*). Jehl and Parkes (1982) referred to a specimen collected "at sea 24 km N of San Benedicto on 3 June 1897." This species was not recorded again within the archipelago until we observed a single individual standing among the Laysan Albatrosses on Albatross Beach in December 1999. In December 2000, we found a bird on an egg on the rim of Herrera Crater. Four days later, we stopped at Guadalupe Island (29° 00′ N, 118° 20′ W), Mexico, where military personnel showed us a "black albatross" nesting area, separate from the Laysan colony. Although no albatrosses were present at that time, we were told that there was a fully-feathered chick at that site in 1998, no nesting in 1999, and, at the time of our visit in 2000, a pair had been visiting the site every afternoon. From this we infer that this species also breeds on Guadalupe. These are the first reported breeding records for this species east of the Hawaiian Islands.

Wedge-tailed Shearwater (*Puffinus pacificus*). This species has declined considerably over time (Table 1). Anthony (1900) reported "thousands upon thousands" circling above the island at dusk in May 1897, and the south end of the island riddled with their burrows. It is clear that the decline and failure to recover of this species is directly related to the eruption; the "ash heap," where most of the nesting was concentrated before the eruption, was buried by Bárcena Crater. Since the eruption, although there has never been a systematic survey, much smaller numbers have been reported staging around the island in the evening. Brattstrom and Howell (1956) reported about 600 individuals in March 1953. Other, more recent estimates have been similar: 363 in April 1981 (Jehl and Parkes 1982) and "several hundred" in April 1990 (Santaella and Sada 1991). Based on the number of nesting burrows we found concentrated around the rim of Herrera Crater, and scattered along the ridges of the northern canyons, we provisionally estimate the breeding population to be about 1,000 pairs.

Townsend's Shearwater (*P. auricularis*). Anthony (1898, 1900) found small colonies, each consisting of "not over a dozen" burrows in May 1897. Kaeding (1905) was at San Benedicto on the same expedition but reported a "large colony." None has been found breeding on the island since the 1952 eruption, and Jehl (1982) suggested that this species may have been extirpated. However, Santaella and Sada (1991) saw 20 individuals that seemed to be heading toward the top of the island at dusk in April 1990, and we saw a pair that appeared to be departing the island at dawn in December 1998. A small population may still breed on the island.

Red-billed Tropicbird (*Phaethon aethereus*). In December 2000, this species was noticeably more abundant than on any of our previous visits and we estimated a breeding population of 200 pairs. At that time birds seemed to be occupying every potential nest site on the island including those being investigated by *P. rubricauda* (see below). It apparently is a winter breeder; birds have been recorded on eggs in November (1953, 1990) and December (1999, 2000), with half grown chicks in March (1988), and a nearly fledged chick in April (1978); the exception was a large downy chick in December 1999.

Red-tailed Tropicbird (*P. rubricauda*). This species probably is a recent colonizer. It was first recorded in February 1988 when Howell and Webb (1990) observed birds courting and apparently scouting nest sites. One month later, we saw birds displaying, including one that occupied a potential nest cavity <2 m from a nesting Red-billed Tropicbird. *P. aethereus* currently outnumbers *P. rubricauda* at least by a factor of ten and the two species may compete for nest sites. Although it probably does breed at San Benedicto, until a bird is found with a chick or egg, Red-tailed Tropicbird must be considered a hypothetical breeder in the eastern Pacific. We estimate the total population at San Benedicto to be about 10 pairs.

Masked Booby (*Sula dactylatra*). Currently this is the most abundant nesting species, although prior to the eruption it was vastly out-

TABLE 1. Historical and present status of breeding seabirds at San Benedicto Island, Mexico. Values are total number of individuals present (number of nesting pairs estimated). P = present, "—" = not present (or not mentioned). Maximum counts are indicated in bold.

Survey date	Laysan Albatross	Black-footed Albatross	Wedge-tailed Shearwater	Townsend's Shearwater	Red-billed Tropicbird
March 1889[a]	—	—	—	—	—
May 1897[b]	—	—	**thousands**	**large colony**	common
May 1925[c]	—	—	**thousands**	—	P
March 1953[d]	—	—	hundreds	—	≥39
November 1953[d]	—	—	—	—	P
April 1955[d]	—	—	—	—	39
April 1978[e]	—	—	(**1000**)	—	13
April 1981[f]	—	—	P	—	—
May 1987[g]	3	—	P	—	P
February 1988[h]	11–14	—	—	—	(50–70)
March 1988[i]	≥12	—	hundreds	—	**300** (150)
April 1990[j]	—	—	P	—	50
November 1990[k]	≥4 (1)	—	—	—	(75)
April 1992[l]	9–12 (2–5)	—	(50–100)	—	(≥40–60)
December 1998[m]	≥5	—	—	—	—
December 1999[n]	≥18 (8)	**1**	—	—	(≥15)
December 2000[o]	**21–25 (12)**	**2 (1)**	—	—	100–200 (**200**)

[a] Townsend 1890.
[b] Anthony 1898, 1900; Kaeding 1905.
[c] Hanna 1926, McLellan 1926.
[d] Brattstrom and Howell 1956, Brattstrom 1963.
[e] RLP unpublished data, Jehl and Parkes 1982; RLP spent 10 h on island.
[f] Jehl and Parkes 1982.
[g] RLP unpublished data; spent 1 h on island.
[h] Howell and Webb 1990.
[i] RLP unpublished data; spent 6 h on island.
[j] Santaella and Sada 1991.
[k] RLP unpublished data; photographed island from air, spent 4 h on island.
[l] S. Howell unpublished data; spent 24 h on the island.
[m] RLP unpublished data; photographed island from air, no time on island.
[n] RLP unpublished data; photographed island from air, spent 4 h on island.
[o] RLP unpublished data; photographed island from air, spent 5 h on island.
[p] Breeding unconfirmed.

numbered by the Red-footed Booby (see General Discussion). From aerial photos we counted 2,185 pairs in 1998, 1,887 pairs in 1999, and 1,988 pairs in 2000. Approximately 75% occupied the floor of Herrera Crater; another 15% were in North Valley (Fig. 1). We have not included in Table 1 Brattstrom's (1963) estimate of 8,100 in August 1961 because it was made from the air and included 7,000 from the lava delta, an area where this species does not breed and rarely roosts. Masked Boobies have a variable breeding schedule on San Benedicto; eggs have been found every month that the island has been visited (February through May, November, and December). During some visits, all stages of nesting were recorded (March 1988, December 1999 and 2000); at other times, breeding appeared to be fairly synchronous (e.g., April 1978, when most nests had downy chicks).

Nazca Booby (*S. granti*). Although this species only recently has been recognized as distinct from the Masked Booby (Pitman and Jehl 1998), we first recorded an "orange-billed" Masked Booby (i.e., *S. granti*) at a nest in 1978. Our high count was in December 2000 when 30 nests at the Punta Observer colony (Fig. 1) contained eggs, chicks, or recently fledged young; two other birds were on nests in the northwest corner of the island, and another individual was on a nest among Masked Boobies near Herrera Crater. We estimate a breeding population of about 50 pairs. Hybridization between *S. granti* and *S. dactylatra* appears to occur to a limited extent on the island. Howell and Webb (1990) reported a mixed pair; during our surveys we

TABLE 1. Extended

Red-tailed Tropicbird	Masked Booby	Nazea Booby	Brown Booby	Red-footed Booby	Great Frigatebird	Magnificent Frigatebird
—	P	—	P	P	numerous	—
—	common	—	common	**abundant**	**thousands**	—
—	P	—	P	numerous	large numbers	—
—	30	—	2	—	10	—
—	535	—	6	2	150–200 (58–116)	—
—	1067	—	11	—	398	—
—	(1500–2000)	P	23 (4)	877 (**100**)	100 (25)	P
—	2000 (1000)	—	20	400	100 (50)	several
—	P	—	P	P	—	≥1
2–5	(585–600)	4	(75–100)	(54)	(100)	12–14 (2)
≥6	**2500** (1017)	P	300 (62)	200	350 (150)	≥5
P	P	—	P	P	≥100	6
4	P	≥**32** (**50**)	(≥50)	(≥50)	≥200 (≥30)	≥6
(1–2)	(600–800)	2	(50–100)	(**50–100**)	(**150–200**)	(**5–10**)
—	(**2185**)	—	P	P	P	P
2	(1887)	≥3 (≥2)	P	(50)	P	—
7–9 (**10**)[p]	(1988)	(**50**)	**300–400** (**300**)	200–300	600 (**165**)	**100**

saw two mixed pairs and four other adults with what appeared to be intermediate-colored bills. Brown Booby (*S. leucogaster*). This species appears to be more abundant now than prior to the eruption; our highest estimate was 300 pairs in December 2000 (Table 1). The breeding season is protracted and we usually found nesting in all stages. Based on the plumage of adult males, at least two races of Brown Booby breed on the island: a white-headed form and a dark-headed form (Fig. 2). White-headed races of this pantropical species occur only in the eastern Pacific with the most extreme examples (as in Fig. 2, left) occurring only on Clipperton Island (10° 18′ N, 109° 13′ W) and sometimes referred to as *S. l. nesiotes* (Nelson 1978). The dark-headed form at San Benedicto (Fig. 2, right) doubtless immigrated from the central Pacific because it is not known to breed anywhere else in the eastern Pacific (B. Tershy pers. comm., RLP pers. obs.). Its bill color and plumage is very similar to *S. l. plotus* that occurs, for example, on Johnston Atoll (16° 45′ N, 169° 31′ W; RLP and LTB pers. obs.) and throughout the central and western Pacific. Intermediate forms also nest on San Benedicto. These could be immigrants from populations elsewhere in the eastern Pacific (*S. l. brewsteri* from the Gulf of California, or *S. l. etesiaca* farther south) or hybrids of the two extreme forms.

Red-footed Booby (*S. sula*). Prior to the 1952 eruption, this was by far the most abundant booby on the island (Anthony 1898, Kaeding 1905, Hanna 1926), but since the eruption the Masked Booby has taken its place; recent estimates all have been about 60 nesting pairs (Table 1). This species has a protracted breeding season at San Benedicto; nests containing fresh eggs, chicks, and ready-to-fledge young have been observed in November, December, February, and April (Howell and Webb 1990, this study).

Great Frigatebird (*Fregata minor*) and Magnificent Frigatebird (*F. magnificens*). All visitors to the island recorded frigatebirds but it was not until 1978 that the presence of two species was recognized (Jehl and Parkes 1982). In Table 1, for convenience, we included all unidentified frigatebird counts prior to 1978 under *F. minor*. Contrary to Jehl and Parkes (1982), frigatebirds do regularly appear at islands far from nesting colonies (see Bowler et al. 2002). For example, at Clipperton Island, we have at times counted over 1,000 frigatebirds, mostly *F. minor* but with some *F. magnificens* usually present. Even though adults are always present, and *F. minor* males sometimes display inflated gular sacs, frigatebirds have never been known to nest at Clipperton (Stager 1964; RLP pers. obs.). Similarly, at San Benedicto, in addition

FIG. 2. Two different forms of adult male Brown Boobies nesting at San Benedicto Island, Mexico, on 3 December 1999. (Left) A white-headed form resembling *Sula leucogaster nesiotes* from Clipperton Island; this bird was with a chick. (Right) A dark-headed form (identified as a male by voice and blue facial skin color) similar to *S. l. plotus* from the central Pacific; this bird was on eggs. Photographs by R. L. Pitman.

to a breeding population of about 165 pairs of *F. minor*, there is an annually and seasonally fluctuating population of nonbreeders that appears only to roost there. In December 2000, the latter group was about 200 birds. The only confirmed nesting records of *F. magnificens* were two pairs in February 1988 (Howell and Webb 1990) and 5–10 pairs in April 1992 (S. N. G. Howell unpubl. data). We never observed nesting, but several males were displaying in a *F. minor* colony in December 2000. At that time an estimated 100 other individuals were present at the island, probably roosting only as described above.

Brown Noddy (*Anous stolidus*). Within the archipelago, this species is known to breed only at Roca Partida and on O'Neal Rock at Socorro; there are no previous records from San Benedicto. We saw a pair flying around the north end in November 1990, and a single bird in December 2000. A few pairs could breed on the cliff faces or offshore stacks but confirmation is lacking.

General discussion.—With four species of boobies, two frigatebirds, and two tropicbirds, the diversity of breeding pelicaniforms at San Benedicto Island is, to our knowledge, unrivaled anywhere in the world. Although the island continues to be uninhabited by humans and free of introduced predators, it has not been totally free of human disturbance. For example, in March 1988 we found that much of the northern part of the island had been burned, there are old fragments of exploded ordnance on the island (presumably from military target practice), and sportfishing boats that regularly ply the nearshore waters inadvertently catch and drown unknown numbers of young boobies and frigatebirds with their trolling gear (RLP pers. obs.). However, the overall effects of these activities appear to have been relatively minor, which provides us with an opportunity to consider some of the natural avifaunal changes that have occurred there over the past century.

Currently, there still are only marine birds breeding on the island. Brattstrom (1963) suggested that 99% of the seabirds on San Be-

nedicto were killed outright by the 1952 eruption, but the prevalence of asynchronous breeding that we observed makes it unlikely that a single event could kill off such a large percentage of the population. There have, however, been changes in the species composition and relative abundance of the breeding birds, and these changes fall into two categories: responses to the 1952 eruption, and colonizations by central Pacific species.

The most significant population change has been the Masked Booby replacing the Red-footed Booby as the most abundant sulid on the island (Jehl and Parkes 1982). As an example, when egg collector E. Harrison (unpubl. data) visited in April 1940, he collected egg sets from 103 Red-footed Boobies, 39 Masked Boobies, and 11 Brown Boobies. Changes in the island flora related to the 1952 eruption may explain this shift. Red-footed Boobies usually nest in trees or shrubs while Masked Boobies are ground nesters (Brattstrom 1963, Nelson 1978). Prior to the eruption, the most conspicuous plant on the island was a grass (*Cenchrus myosuroides*). It grew to 2 m high in dense stands and was "very common in the flats" (Johnston 1931). It became extinct on the island after the eruption (Levin and Moran 1989) and Masked Boobies now nest in the flats.

In addition to pelicaniforms, one or two species of shearwater currently breed on the island. As expected for burrow nesters, the populations of both declined initially after the eruption, but they failed to recover, which raises some conservation issues. San Benedicto is the only island in the eastern Pacific where Wedge-tailed Shearwaters breed and that population appears to be morphologically distinct. Wedge-tailed Shearwaters are polymorphic and compared to central Pacific populations, light morphs from San Benedicto are smudgy and not as cleanly marked, dark morphs are lighter brown, and intermediate birds occur more commonly. An investigation into the taxonomic status of this small, isolated population should be an important conservation priority. As for Townsend's Shearwater, even a small colony at San Benedicto could be important for this species' survival, given that the only other breeding populations of this Revillagigedos endemic, at Socorro and Clarión islands, currently are threatened by introduced predators (Collar et al. 1994).

Another, perhaps positive, effect of the eruption was the elimination of ravens from the island, which were common prior to the eruption (Anthony 1898, Kaeding 1905). Brattstrom and Howell (1956) suggested that the ravens on San Benedicto were not resident but instead visitors from Clarión. However, no ravens have been observed at San Benedicto since the eruption, so it is likely they were residents (Jehl and Parkes 1982). Anthony (1898) commented that it was odd that ravens were common on both Clarión and San Benedicto, but absent from the much larger Socorro Island. This may be due to the fact that the main seabird colonies in the Revillagigedos are on Clarión and San Benedicto, which could provide opportunities for ravens to feed on chicks, eggs, and regurgitated food. The extent to which ravens could have affected nesting seabirds at San Benedicto is unknown, but may have been substantial. McLellan (1926), for example, reported that ravens at Clarión "were seen hovering over shearwater burrows, and it was thought that they feed to some extent on young shearwaters and boobies." Similarly, Santaella and Sada (1991) suggested that ravens associated with Red-footed Booby colonies on Clarión were waiting for opportunities to steal eggs or chicks.

Perhaps a more dramatic change in the San Benedicto avifauna, has been the recent colonization by at least two, and possibly as many as four, species of central Pacific seabirds. The Laysan and Black-footed albatrosses that colonized the island within the past 15 years almost certainly came from colonies in the Hawaiian Islands where the vast majority of both species breeds (Gales 1998). Laysan Albatrosses apparently were prospecting for nest sites in the eastern Pacific as early as the mid-1970s (Pitman 1985), but did not nest on San Benedicto until the late 1980s. The Black-footed Albatross first bred on the island in 2000. A third central Pacific species, Red-tailed Tropicbird, also appears to have colonized San Benedicto recently, possibly in the 1980s, and at least some of the Brown Boobies that nest on the island undoubtedly came from central Pacific colonies, although the date of colonization is unknown.

The cause(s) for these breeding range ex-

tensions is not known, but the fact that there are several species involved suggests a change in the marine environment. Further investigations at sea and at other breeding islands in the Pacific will be necessary to determine if this avifaunal shift is part of a long term, basin-wide trend, or a short term or localized anomaly. Currently, climate change and its potential effect on ocean ecosystems, including the composition of seabird communities, is a much-debated topic (e.g., Aebischer et al. 1990, Veit et al. 1996, Anderson and Piatt 1999, Oedekoven et al. 2001). One of the best and most cost effective ways of integrating long term changes in oceanographic productivity over a variety of trophic levels will be to continue to monitor seabird colonies with long histories of faunal inventories, colonies such as those on San Benedicto Island.

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APPENDIX

Records of migrant birds at San Benedicto Island. * = new record for San Benedicto, ** = new record for Revillagigedo Islands (see Howell and Webb 1992b, Wehtje et al. 1993, and references cited therein)

*Great Blue Heron (*Ardea herodias*): 1 in March 1988.

*Cattle Egret (*Bubulcus ibis*): 6 in December 2000.

Osprey (*Pandion haliaetus*): 1 in March 1988.

Peregrine Falcon (*Falco peregrinus*): 1 in March 1988, 1 in December 1999, 1 adult in December 2000.

American Kestrel (*Falco sparverius*): 2–3 in March 1988, 2 in November 1990, 3–4 in December 1999.

Golden Plover (*Pluvialis* sp.): 1 in March 1988.

Whimbrel (*Numenius phaeopus*): 1 in March 1988, 1 in November 1990.

Wandering Tattler (*Heteroscelus incanus*): 1 each in May 1987, March 1988, and November 1990.

*Least Sandpiper (*Calidris minutilla*): 2 in November 1990.

**Common Snipe (*Gallinago gallinago*): 1 in December 2000.

*Laughing Gull (*Larus atricilla*): 2 juveniles in December 1999.

California Gull (*Larus californicus*): a first-year bird, long dead on beach in March 1988.

*Short-eared Owl (*Asio flammeus*): 1 in December 2000.

**White-throated Swift (*Aeronautes saxatalis*): 1 in December 1999.

*Northern Rough-winged Swallow (*Stelgidopteryx serripennis*): 4 in December 2000.

**Violet-green Swallow (*Tachycineta thalassina*): 2 in December 2000.

**Tree Swallow (*Tachycineta bicolor*): 1 in November 1990; 6 in December 2000.

Barn Swallow (*Hirundo rustica*): 1 in November 1990, 2 in December 1999, 1 in December 2000.

*Northern Mockingbird (*Mimus polyglottos*): 1 in December 1999.

*Yellow-rumped Warbler (*Dendroica coronata*): 23 in one flock in March 1988.

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SPECIES LIMITS IN OLIVE-BACKED FOLIAGE-GLEANERS (*AUTOMOLUS*: FURNARIIDAE)

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ABSTRACT.—New information on the vocalizations and behavior of populations of the Olive-backed Foliage-gleaner (*Automolus infuscatus*), along with analysis of biometric and plumage characters, reveal that it actually consists of at least two biological species: a form that is restricted to southeastern Amazonia, south of the Amazon and east of the Rio Madeira; and a group that occupies much of the remainder of humid lowland forest in Amazonia and the Guianan region. The southeastern form, although cryptically similar morphologically to other southern Amazonian subspecies of *Automolus infuscatus*, is highly differentiated in all vocal characters. Its distribution overlaps the Rondônia, Pará, and Belém centers of endemism. The remainder of the populations currently considered part of the *infuscatus* group are further differentiated into two subgroups: a northern Guianan group and a southern-western group, the member taxa of which are weakly differentiated from one another, but which differ from members of the other group in plumage, biometric, and vocal characters. The significance of these differences with respect to species limits may depend on the species concept used. Current evidence would support recognition of the two groups as separate phylogenetic species in addition to the southeastern species, but is considered insufficient to support recognition of more than two species under a biological species concept.
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The genus *Automolus* is a group of fairly large, mostly drab plumaged foliage-gleaners (subfamily Philydorinae), which comprises 6–11 species. Vaurie (1980) included the species *rectirostris* and *erythrocephalus* in his expanded view of the genus, but most recent authors (Peters 1951; Meyer de Schauensee 1966, 1970; Ridgely and Tudor 1994) have recognized those two species in the separate genus *Hylocryptus*. Kratter and Parker (1997) convincingly demonstrated that *dorsalis* belongs with *Anabazenops* rather than *Automolus*, and strong arguments have been made for the transfer of *ruficollis* from *Automolus* to *Syndactyla* (Parker et al. 1985, 1995; Fjeldså and Krabbe 1990; Ridgely and Tudor 1994). More work also is needed to clarify the relationships of *Automolus roraimae*, whose inclusion in the genus has been questioned (Ridgely and Tudor 1994, Kratter and Parker 1997). This leaves a core of six currently recognized species (*leucophthalamus*, *infuscatus*, *rubiginosus*, *ochrolaemus*, *rufipileatus*, and *melanopezus*) comprising the genus *Automolus*.

One of the most widespread members of the genus is the Olive-backed Foliage-gleaner (*A. infuscatus*), which inhabits lowland humid forest throughout much of Amazonia and the Guianan region. Although there are five named subspecies of *A. infuscatus* (Peters 1951), geographic variation within the species has been categorized as "slight" and "not significant" (Vaurie 1980), and no recent authors of either technical works or popular field guides have commented on it.

In August 1991, while conducting field work in the Alta Floresta region of Mato Grosso, Brazil, I noticed the local population of Olive-backed Foliage-gleaners (*A. i. paraensis*) varied dramatically in songs and calls from populations with which I was familiar in Venezuela. Subsequent communication with colleagues revealed that in 1986, T. S. Schulenberg and D. F. Stotz had tape recorded unfamiliar voices of Olive-backed Foliage-gleaners from the middle Rio Jiparaná in eastern Rondônia, Brazil, that matched those I had recorded at Alta Floresta. T. A. Parker also had independently noted the vocal distinctiveness of the Alta Floresta birds on his first trip to the region in 1989 (T. A. Parker pers. comm.). Intrigued by the vocal distinctiveness of birds that appeared, under field conditions, to be "typical" Olive-backed Foliage-gleaners in plumage characters, I began investigating vocal and morphological variation among all of the recognized subspecies in the complex.

In this paper I present new evidence of vocal differences among populations of Olive-

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backed Foliage-gleaners, and re-evaluate geographic variation in plumage and biometric characters within the species. I demonstrate that the subspecies *A. i. paraensis* is sufficiently differentiated to be considered a biological species distinct from other members of the group.

METHODS

I observed and tape recorded "Olive-backed" Foliage-gleaners near Alta Floresta, Mato Grosso, Brazil (yearly visits in August, September, or October, 1991–1999); at Caxiuanã Forest Reserve, Pará, Brazil (August 1999); at São Gabriel da Cachoeira, Amazonas, Brazil (January 1995 and August 1999); Tiputini Biodiversity Station, Napo Province, Ecuador (August 1996); Tambopata Research Center, Madre de Dios, Peru (August 1994); and at multiple sites in Amazonas, Brazil (1991–2000) and edo. Amazonas and edo. Bolívar, Venezuela (1991–1998). All measurements used in behavioral data (distances, heights, etc.) are estimates. Mapped distributions in this paper are based on label data from specimens that I examined, and by more recent records documented with tape recordings. These localities, along with the type localities for each taxon, were entered into a geographic information system (Isler 1997) and mapped by M. L. Isler.

I assume that vocalizations of foliage-gleaners, like those of other suboscines, are mostly or entirely inherited (Kroodsma 1984, 1989; Kroodsma and Konishi 1991), and consequently provide potentially important characters for systematic study (Lanyon 1978, Isler et al. 1997, Krabbe and Schulenberg 1997, Zimmer 1997). To analyze vocalizations, I assembled recordings of *Automolus infuscatus* from across its geographic range, made auditory comparisons, and visually compared spectrograms of all individuals recorded. Songs selected for illustration as spectrograms in this paper were deemed representative based on visual comparison of spectrograms of the large sample. I also examined my own collection of recordings of songs and calls of *A. leucophthalamus*, *A. rubiginosus*, *A. ochrolaemus*, *A. rufipileatus*, and *A. melanopezus* for qualitative comparison with the vocalizations of *A. infuscatus*. This involved both auditory comparison and superficial visual comparison of spectrograms. Locations and recordists for all recordings of *A. infuscatus* examined are given in Appendix 1. For comparison, vocalizations were categorized as loudsongs, calls, and long calls. Loudsongs were consistently patterned multinote vocalizations (Isler et al. 1997) given seemingly in the context of territorial advertisement. Vocalizations characterized as calls usually were structurally simple (typically involving well-spaced repetition of identical notes or pairs of notes), and most often were given in the context of contact notes between mates, or as aggression calls during territorial conflicts with conspecifics, or in response to tape playback. Exceptions are noted in the results, below. Vocalizations categorized as long calls were infrequently given series of mostly identical single note calls delivered in rapid succession, the context of which was unclear. My tape recordings were made with a Sony TCM-5000 recorder with Sennheiser ME-80 and MKH-70 shotgun microphones. Spectrograms used in illustrations were made by P. R. Isler on a Macintosh G4 computer using Canary version 1.2.1 (Bioacoustics Research Program, Cornell Lab. of Ornithology, Ithaca, New York), Canvas graphics software (version 5.0.3, Deneba Software, Miami, Florida), and a Hewlett Packard Laserjet 6MP printer.

To identify morphological differences, I examined representative specimens of *A. i. infuscatus* (n = 83), *A. i. purusianus* (n = 40), *A. i. paraensis* (n = 83), *A. i. badius* (n = 57), and *A. i. cervicalis* (n = 39). These specimens are housed at the Academy of Natural Sciences of Philadelphia, Philadelphia (ANSP); Carnegie Museum, Pittsburgh (CM); Field Museum of Natural History, Chicago (FMNH); Los Angeles County Museum of Natural History, Los Angeles (LACM); Louisiana State Univ. Museum of Natural Science, Baton Rouge (LSUMZ); National Museum of Natural History, Washington, D.C. (USNM); and the Peabody Museum of Natural History, Yale Univ., New Haven (YPM) (Appendix 2). A wing rule with a perpendicular stop at zero was used to measure wing chord (wing), tail length (tail), and hind toe length (hind toe), and dial calipers were used to measure tarsus length (tarsus), culmen length from the anterior end of the nares to the tip (culmen), bill depth at the anterior end of the nares (bill depth), bill width at the anterior end of the nares (bill width), and hind claw length (hind claw). All measurements made with calipers were to the nearest 0.1 mm; those taken with the wing rule were to the nearest 0.5 mm. Measurement terminology conforms with that used by Pyle et al. (1987). Plumage was described from specimens and compared to a standard color reference (Smithe 1975).

General linear models were used to investigate gender-corrected differences among the five subspecies for each of the eight characters measured. Residual diagnostics indicated no violations of the general linear model assumptions of error normality and constant variance. Bonferonni multiple comparisons (two-tailed t-test) with a family error rate of 5% were used to compare pairwise subspecies differences for each variable (Sokal and Rohlf 1995). Intervals that do not contain zero indicate a significant difference among the pair of species. Statistical analyses (ANOVA procedure and Bonferonni multicomp procedure) were performed using S-Plus version 4.5 for Windows.

RESULTS

Distribution.—Nominate *A. i. infuscatus* occurs in western Amazonia, from southeastern Colombia south through the lowlands of eastern Ecuador and eastern Peru to Bolivia (Fig. 1). *Automolus infuscatus purusianus* replaces nominate *infuscatus* in western Brazil south of the Solimães (= Amazon), east to the left

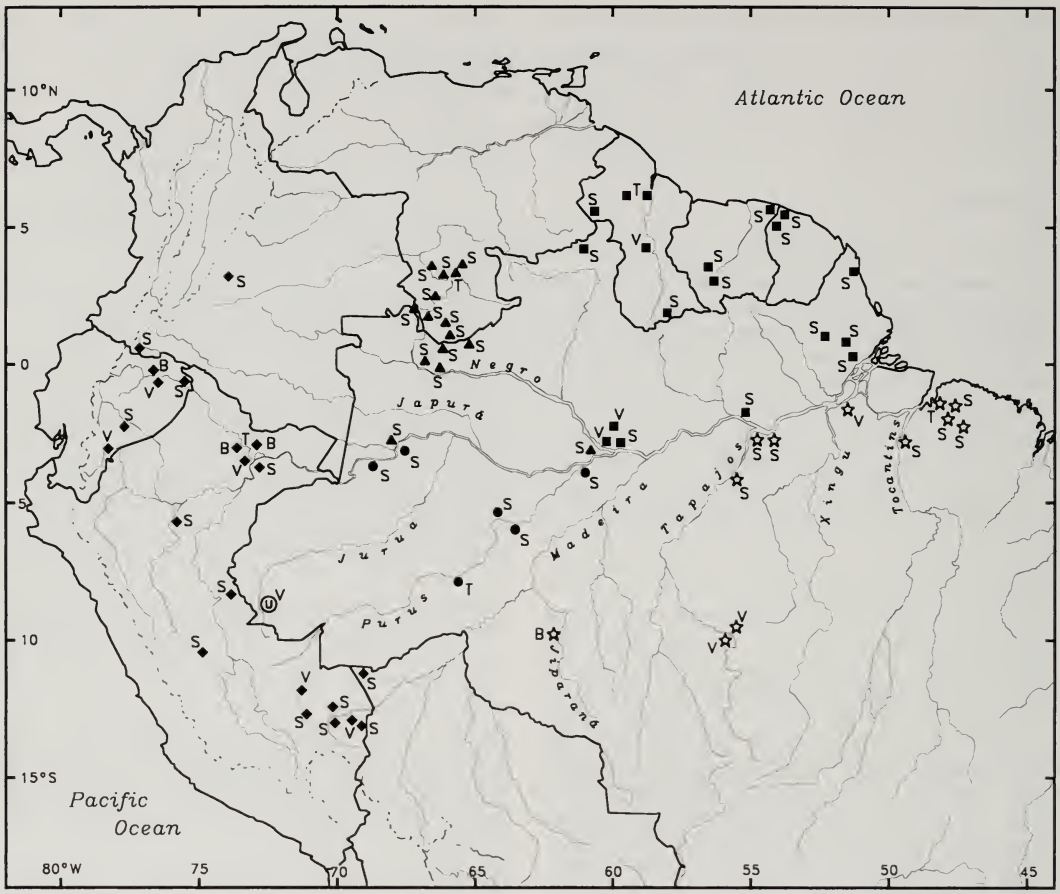

FIG. 1. Distribution of "Olive-backed" Foliage-gleaners (*Automolus infuscatus*) as confirmed by examination of specimens or tape recordings: open stars = *A. i. paraensis*; black diamonds = *A. i. infuscatus*; black circles = *A. i. purusianus*; black triangles = *A. i. badius*; black squares = *A. i. cervicalis*; "T" next to a symbol indicates the type locality for that taxon; "S" next to a symbol indicates specimen confirmation for that taxon; "V" next to a symbol indicates vocal confirmation (tape recording) for that taxon; "B" next to a symbol indicates both specimen and vocal confirmation for that taxon; and "U" in a circle locates Porongaba, Acre, Brazil, from which archived tape recordings could not be identified with certainty (either *A. i. infuscatus* or *A. i. purusianus*).

bank of the Rio Madeira. It probably contacts *A. i. infuscatus* in extreme western Brazil, possibly in the upper regions of the Rio Juruá or Purus, but this has yet to be determined. *Automolus i. paraensis* occurs south of the Amazon and east of the Rio Madeira to the right bank of the Rio Tocantins. North of the Amazon, the complex is represented by two subspecies: *A. i. badius*, from central edo. Bolívar, Venezuela west to the upper Rio Negro region of eastern Colombia and south through northwestern Brazil along the west bank of the Rio Negro to its mouth; and *A. i. cervicalis*, from northeastern edo. Bolívar, Venezuela east through French Guiana and in Brazil north of the Amazon and east of the Rio Negro through Amapá. These two north bank forms may contact one another in northern Brazil above the confluence of the Rio Branco and Rio Negro, but this has yet to be determined.

Habitat.—All forms of *A. infuscatus* are found in lowland humid forest below 1,000 m. They occur in *várzea*, transitional, and *terra firme* forest, but generally are more common in the latter habitat.

Behavior.—All forms of *A. infuscatus* occupied the lower to mid-levels of the forest strata, and usually were encountered as mem-

bers of mixed species flocks of insectivores comprised primarily of woodcreepers, other foliage-gleaners, antshrikes (mainly *Thamnomanes* spp.) and antwrens (*Myrmotherula* spp.). My observations of *A. i. badius*, *A. i. cervicalis*, *A. i. infuscatus* and *A. i. paraensis* suggest they are all dead-leaf-searching specialists (>75% of all foraging maneuvers involved searches of dead leaves for arthropods), probing dead leaves suspended in vine tangles and in crowns of understory trees (particularly palms). During these searches, foliage-gleaners clung acrobatically (often upside down) onto palm fronds, vines, or large dead leaves (particularly those of *Cecropia* spp. and species of palms), and probed with their bill for 1–15 s into curled dead leaves. An individual would routinely hold large dead leaves steady with its foot and then tear the leaf apart with its bill, using a variety of hammering and shredding motions. Where mats of many dead leaves were trapped in a tangle or the crown of a palm, foliage-gleaners would use their bill to vigorously toss out one leaf after another in search of prey.

Plumage.—The five subspecies of Olive-backed Foliage-gleaner are so similar in plumage characters that silent birds could easily defy identification in the field. In direct comparison, specimens usually were separable by a combination of dorsal coloration, crown pattern, and the degree of contrast between the crown-nape and back. *Automolus i. badius* is distinctly more reddish dorsally than all other subspecies, the back being between Raw Umber (color #223, capitalized color names from Smithe 1975) and Proutãs Brown (color #121A). The crown and nape feathers have minimally contrasting darker fringes, lending a slight scaly pattern, but the ground color of the crown and nape is uniform with the back. The other subspecies are more truly "olive-backed," with *A. i. infuscatus*, *A. i. paraensis*, and *A. i. cervicalis* all having the back closest to Dark Brownish Olive (color #129), and *A. i. purusianus* being close to this color but perhaps marginally more reddish (closest to Hair Brown, color #119A). Of these forms, *A. i. paraensis* is the most distinctly plumaged. The feathers of the crown and nape are noticeably grayer, contrasting with the brownish olive back. These feathers also have fairly broad dark terminal fringes, which creates a distinct scaly pattern to the crown and nape. Nominate *infuscatus* also has dark terminal fringes to the crown and nape feathers, but the feather centers are brownish olive like those of the back (not distinctly grayer as in *A. i. paraensis*), and the terminal fringes are narrower, with the result that there is less contrast between the nape and back. *Automolus i. purusianus* has much less distinct dark fringing to the crown and nape feathers, and the overall effect is of the crown, nape, and back being uniformly colored (as in *A. i. badius* but less reddish). *Automolus i. cervicalis* has even less dark fringing to the crown and nape feathers, but these are a warmer brown color than the back, and thus, contrast slightly.

All five subspecies have rufescent tails which contrast with the drab upperparts. The contrast is least conspicuous in *A. i. badius*, which is distinctly more reddish dorsally than the other forms. *Automolus i. paraensis* has the tail a deeper rust color than the other forms, the color being between Burnt Sienna (color #132) and Mars Brown (color #223A). All subspecies are similar ventrally, being dingy grayish-buff, with browner flanks and a contrasting creamy-white throat. The only exception is *A. i. badius*, which, although generally similar, is distinctly grayer from the midbreast to the belly.

Size.—Subspecies of *Automolus infuscatus* differed from one another in mean measurements of all characters that were measured (Tables 1, 2; Fig. 2). Between-taxa differences were found in measurements of culmen ($F_{4,284} = 13.3$, $P < 0.0001$), bill depth ($F_{4,279} = 6.6$, $P = 0.0001$), bill width ($F_{4,287} = 3.1$, $P = 0.015$), wing chord ($F_{4,287} = 21.8$, $P < 0.0001$), tail length ($F_{4,285} = 14.3$, $P < 0.0001$), tarsus ($F_{4,285} = 44.6$, $P < 0.0001$), hind claw ($F_{4,285} = 49.3$, $P < 0.0001$), and hind toe ($F_{4,286} = 48.7$, $P < 0.0001$). There were no biometric differences between *A. i. infuscatus* and *A. i. paraensis* (Table 2). *Automolus i. paraensis* and *A. i. infuscatus* differed from *A. i. purusianus* only in wing chord. *Automolus i. badius* and *A. i. cervicalis* differed from one another in culmen length, wing chord, and hind claw length. All other differences reflected a split between smaller taxa from north of the Amazon (*A. i. badius* and *A. i. cervicalis*), and larger taxa whose ranges were predominantly or entirely south

TABLE 1. Means (± SD), ranges, and sample sizes of selected measurements (mm) of the five subspecies of Olive-backed Foliage-gleaner (*Automolus infuscatus*). Significance: * = $P < 0.001$; ** = $P < 0.0001$. Values of *F* and *P* are from ANOVA. Asterisks following a character indicate differences between two or more of the subspecies, after correcting for potential sex differences within taxa.

Characters	*badius*	*cervicalis*	*infuscatus*	*paraensis*	*purusianus*	*F*
Culmen**	14.1 ± 0.6	13.6 ± 0.6	14.2 ± 0.7	14.5 ± 0.7	14.3 ± 0.7	13.3
	12.9–15.6	11.8–15.2	12.5–16.2	13.1–16.6	12.9–15.9	
	(*n* = 50)	(*n* = 37)	(*n* = 82)	(*n* = 83)	(*n* = 39)	
Bill depth**	6.5 ± 0.3	6.6 ± 0.3	6.6 ± 0.3	6.7 ± 0.3	6.7 ± 0.3	6.6
	6.0–7.1	6.1–7.1	6.0–7.2	5.9–7.3	6.1–7.4	
	(*n* = 51)	(*n* = 35)	(*n* = 81)	(*n* = 80)	(*n* = 39)	
Bill width*	5.0 ± 0.2	5.1 ± 0.2	5.2 ± 0.2	5.2 ± 0.2	5.1 ± 0.3	3.1
	4.4–5.6	4.7–5.6	4.7–5.7	4.7–5.7	4.3–5.6	
	(*n* = 52)	(*n* = 37)	(*n* = 82)	(*n* = 83)	(*n* = 40)	
Wing chord**	89.0 ± 3.4	86.3 ± 3.1	90.6 ± 3.7	89.8 ± 3.7	93.1 ± 3.6	21.8
	80.5–95.5	77.5–91	83–98.5	82–97	84.5–100	
	(*n* = 52)	(*n* = 37)	(*n* = 82)	(*n* = 83)	(*n* = 40)	
Tail**	75.0 ± 3.2	75.2 ± 4.0	78.1 ± 4.1	79.1 ± 3.5	78.1 ± 4.2	14.3
	68–82.5	68–85	70–88.5	72–87	71–91	
	(*n* = 52)	(*n* = 37)	(*n* = 82)	(*n* = 81)	(*n* = 40)	
Tarsus**	21.7 ± 0.8	21.6 ± 0.9	22.8 ± 0.8	23.1 ± 0.7	23.0 ± 1.0	44.6
	20.5–23.8	20–23.8	20.3–24.5	21.1–25.5	20.3–25	
	(*n* = 52)	(*n* = 37)	(*n* = 82)	(*n* = 82)	(*n* = 39)	
Hind claw*	7.0 ± 0.3	6.7 ± 0.4	7.5 ± 0.4	7.4 ± 0.3	7.5 ± 0.4	49.3
	6.4–7.6	5.8–7.6	6.5–8.5	6.7–8.1	6.6–8.6	
	(*n* = 52)	(*n* = 37)	(*n* = 82)	(*n* = 82)	(*n* = 39)	
Hind toe**	10.4 ± 0.5	10.2 ± 0.6	11.3 ± 0.6	11.2 ± 0.5	11.3 ± 0.6	48.7
	9.5–11.5	9–11	10–12.5	10–13	10–12.5	
	(*n* = 52)	(*n* = 37)	(*n* = 82)	(*n* = 82)	(*n* = 40)	

of the Amazon (*A. i. infuscatus*, *A. i. purusianus*, and *A. i. paraensis*). In spite of mean differences between taxa, ranges for each of the variables were overlapping, and no taxon could be diagnosed solely on biometric characters (Fig. 2).

Vocalizations.—I assembled recordings of 98 different Olive-backed Foliage-gleaners (55 *A. i. infuscatus*, 30 *A. i. paraensis*, eight *A. i. cervicalis*, three *A. i. badius*, two taxon unidentified), including more than 900 individual songs and 1,100 calls. All subspecies except *A. i. purusianus* were represented.

Spectrographic analysis confirmed my field impressions that *A. i. paraensis* differed strikingly and consistently in all aspects of its vocal repertoire from all other subspecies in the complex. The loudsong of this subspecies (Fig. 3A–D) was a loud series of 2–17 well-spaced, frequency-modulated notes, each of which had a particularly harsh, grating quality. The number of notes and the length of songs varied within a song bout in the same individual. Typical songs contained 4–10 notes (85.2% of all songs; 57% of all songs composed of ≤6 notes) and began with a differentiated note that was longer than all subsequent notes in the song (*jureet-reetreetreetreet* or *breek brik brik brik brik*). Individuals occasionally sang longer songs (Fig. 3C) of 11–17 notes (14.8% of all songs recorded), that began with a less differentiated first note followed by a longer than average interval before the next note, and were then evenly paced through the remainder of the song. These songs give the impression of a grating laugh. Within a song bout, individuals tended to sing 4–5 consecutive songs with an identical number of notes before adding or subtracting notes. When presented with tape playback of short songs (3–6 notes), birds usually responded with distinctly longer songs, but when presented with tape playback of longer songs (≥10 notes) they usually reverted to short songs. Both short and long responses to playback fell within the same range of notes found in natural (unsolicited) songs. The most common call was a loud, single-noted *quip* or

TABLE 2. Bonferroni multiple comparisons of eight biometric variables (mm) between the five subspecies of Olive-backed Foliage-gleaner (*Automolus infuscatus*). All measurements are from museum specimens. For each intertaxon comparison, the *t*-values are listed above the associated values of *P*. Degrees of freedom for *t*-values = 284 (culmen), 279 (bill depth), 287 (bill width, wing chord), 285 (tail, tarsus, hind claw), and 286 (hind toe). Differences between taxa are considered significant (*) only when $P < 0.005$, to achieve a Bonferroni family error rate of 0.05.

	Culmen	Bill depth	Bill width	Wing	Tail	Tarsus	Claw	Toe
badius-cervicalis	3.27	−1.20	−0.87	3.63	−0.27	0.71	4.54	1.80
	0.001*	0.230	0.383	0.000*	0.787	0.479	0.000*	0.073
badius-infuscatus	−1.87	−2.64	−2.86	−3.02	−4.93	−8.19	−8.26	−9.36
	0.063	0.009	0.004*	0.003*	0.000*	0.000*	0.000*	0.000*
badius-paraensis	−3.80	−4.01	−2.81	−1.95	−6.15	−10.29	−5.69	−8.84
	0.002*	0.000*	0.005	0.053	0.000*	0.000*	0.000*	0.000*
badius-purusianus	−1.93	−4.36	−1.35	−5.62	−4.05	−7.74	−6.11	−7.54
	0.055	0.000*	0.178	0.000*	0.000*	0.000*	0.000*	0.000*
cervicalis-infuscatus	−5.27	−1.02	−1.61	−6.66	−4.13	−8.00	−12.33	−10.29
	0.000*	0.307	0.108	0.000*	0.000*	0.000*	0.000*	0.000*
cervicalis-paraensis	−7.05	−2.28	−1.58	−5.70	−5.25	−10.07	−10.07	−9.90
	0.000*	0.024	0.114	0.000*	0.000*	0.000*	0.000*	0.000*
cervicalis-purusianus	−4.88	−2.85	−0.42	−8.60	−3.46	−7.81	−9.88	−8.67
	0.000*	0.004*	0.677	0.000*	0.000*	0.000*	0.000*	0.000*
infuscatus-paraensis	−2.22	−1.58	0.04	1.19	−1.41	−2.54	2.79	0.46
	0.027	0.114	0.970	0.236	0.159	0.012	0.006	0.649
infuscatus-purusianus	−0.40	−2.35	1.16	−3.35	0.14	−0.95	0.89	0.37
	0.692	0.020	0.247	0.001*	0.886	0.344	0.375	0.712
paraensis-purusianus	1.40	−1.04	1.12	−4.27	1.29	1.14	−1.37	−0.004
	0.161	0.301	0.262	0.000*	0.196	0.256	0.171	0.997

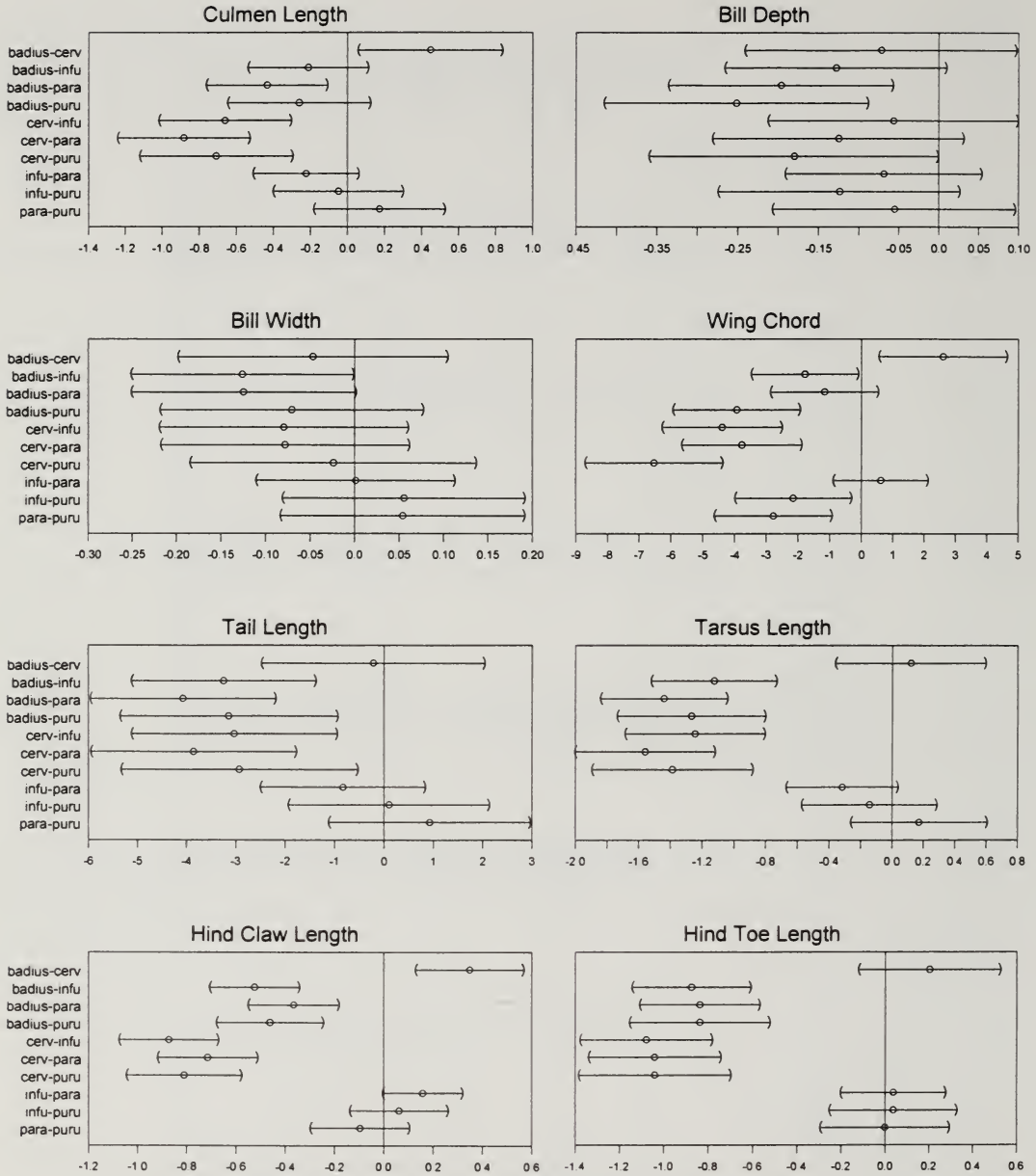

FIG. 2. Graphical display of Bonferonni multiple comparisons of eight biometric variables (as measured from museum specimens) between the five subspecies of Olive-backed Foliage-gleaner (*Automolus infuscatus*). Test values are in Table 2. Codes for the taxa are: badius = *A. i. badius*; cerv = *A. i. cervicalis*; infu = *A. i. infuscatus*; para = *A. i. paraensis*; puru = *A. i. purusianus*. Intervals that do not contain zero indicate a significant difference among the pair of subspecies being compared.

queep, with a distinctly liquid quality (Fig. 3E, F). Less frequently given was a similar sounding two-noted call in which the first and second notes were slightly differentiated (Fig. 3G). These two calls were given as contact calls by both members of a foraging pair, but also were delivered in an aggressive context in response to tape playback or the presence of neighboring conspecifics. The long call was a series of 4–10 *quip* notes that accelerated

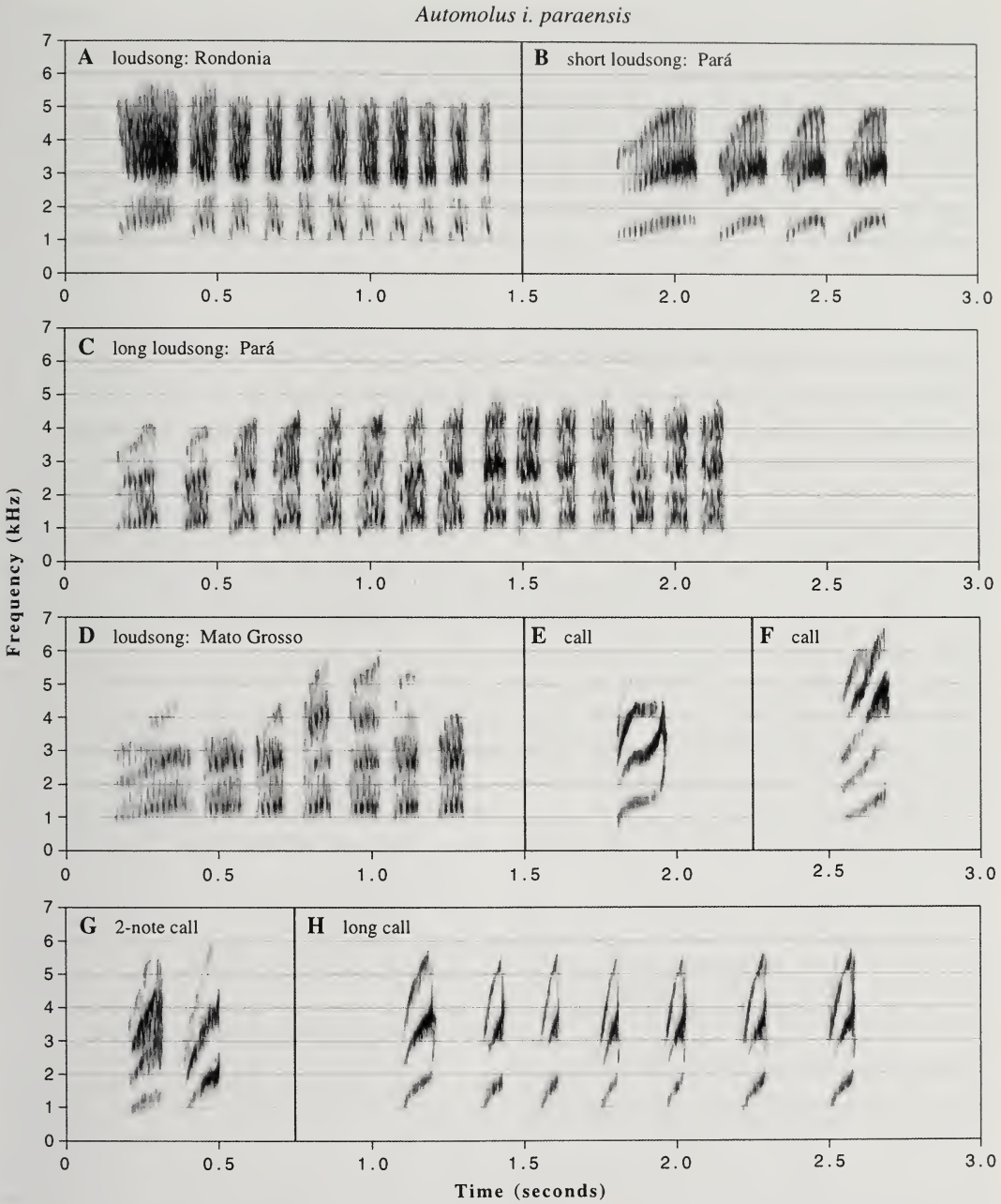

FIG. 3. Types of vocalizations of *Automolus infuscatus paraensis*: (A) loudsong from Rondônia, Brazil (T. S. Schulenberg recording, LNS #43362); (B) short loudsong from Pará, Brazil; (C) long loudsong from Pará, Brazil; (D) loudsong from Mato Grosso, Brazil; (E) *queep* call from Pará, Brazil; (F) *queep* call from Mato Grosso, Brazil; (G) two-note call from Mato Grosso, Brazil; and (H) long call from Mato Grosso, Brazil. Except as noted, all recordings by K. J. Zimmer.

after the initial note and then slowed toward the end (Fig. 3H). Birds from Rondônia, Mato Grosso, and Pará were similar in all vocalizations. Variations in songs (Fig. 3) are indicative of variations between songs of a single individual, as well as of variations among individuals of a single population. They do not reflect any consistent geographic variation that I could identify.

In contrast, the loudsongs of *A. i. infuscatus*, *A. i. cervicalis*, and *A. i. badius* were slightly descending rattles that were similar to one another in pattern and pitch, but differed in length (Fig. 4). The rattle of each subspecies was an evenly paced series of rapidly delivered similar notes that began at about 4 kHz and leveled off at about 3 kHz. The loudsongs of each of these three subspecies were similarly paced, and were delivered at a rate too fast for the human ear to clearly distinguish individual notes. The loudsongs of *A. i. infuscatus* (Fig. 4A–C) averaged about twice as many notes as those of *A. i. cervicalis* (Fig. 4D–F) and *A. i. badius* (Fig. 4G). There were no appreciable differences between the songs of the latter two subspecies, nor was there evidence of consistent geographic variation in the songs of either *A. i. infuscatus* or *A. i. cervicalis*.

The calls of *A. i. infuscatus*, *A. i. badius*, and *A. i. cervicalis* also were highly differentiated from those of *A. i. paraensis*. The most commonly heard call from *A. i. infuscatus* is a two-noted *chik-uh* or *chik-it* in which the first note is higher pitched than the second (Fig. 5A, B). This call frequently was given by both members of a foraging pair, and functioned as a contact call or a heightened awareness call. It also was delivered repeatedly by birds responding to tape playback. Nominate birds also gave a sharp, squeaky, single-noted call that was similar to the first note of the two-noted call (Fig. 5C, D), as well as a hard rattle call that was similar to an abbreviated, flatter version of the loudsong (Fig. 5E). This latter vocalization was given most often in an aggressive context, particularly when birds responded to tape playback. The single-noted call is similar to the alarm squeaks given by the various species of leaftossers (*Sclerurus* spp.). The long call of nominate birds (Fig. 5F) begins with a differentiated, drawn out first note, followed by a series of ≥5 shorter identical notes given in rapid succession (*skeew wekwekwekwekwek*). Populations of nominate *infuscatus* from Ecuador, Peru, and Bolivia had similar calls.

The most frequently given calls of both *A. i. badius* and *A. i. cervicalis* (Fig. 5G, H) were two-noted, with the first note being shorter and higher-pitched (*chik-qwaah*). This call is markedly similar to the primary songs of some spinetails of the genus *Synallaxis*. It is somewhat similar to the two-noted call of *A. i. infuscatus* (Fig. 5A, B), but differs in being slower, with the two notes more strongly differentiated from one another. Differences in tonal quality between the two-noted calls of nominate birds and those of *A. i. badius* and *A. i. cervicalis* are reflected in the obvious differences in note shape as seen in the spectrograms. Single-note *chik* or *stit* calls (Fig. 5I) of the latter two subspecies also were similar, and differed from those of nominate birds in being less squeaky sounding. As was true with *A. i. infuscatus*, the two-note and one-note calls of *A. i. badius* and *A. i. cervicalis* appeared to function as contact calls between mates, as heightened awareness calls when birds were alarmed by my presence, and as aggression calls when birds were responding to tape playback. Two additional calls were noted for *A. i. badius*: a harsh *chek* (Fig. 5J); and a harsh, downslurred *cheer* (Fig. 5K). The small samples of *A. i. badius* and *A. i. cervicalis* recordings did not include long calls, nor did I note such calls in the field. Whether this reflected an absence of such a vocalization type from the repertoires of the two north bank forms, or was merely an artifact of sampling error, has yet to be determined.

A recording of a pair of birds from the upper Rio Juruá (Porongaba, Acre, Brazil) may be of *A. i. purusianus*, but the subspecific identity of Olive-backed Foliage-gleaners from that region is uncertain. The recorded vocalizations, which include songs, single-note calls, and two-note calls, are indistinguishable from those of nominate *A. infuscatus*.

Plumage, biometric, and vocal characters distinguishing the five subspecies are summarized in Fig. 6.

DISCUSSION

Spectrographic comparison of vocal characters reveals that Olive-backed Foliage-

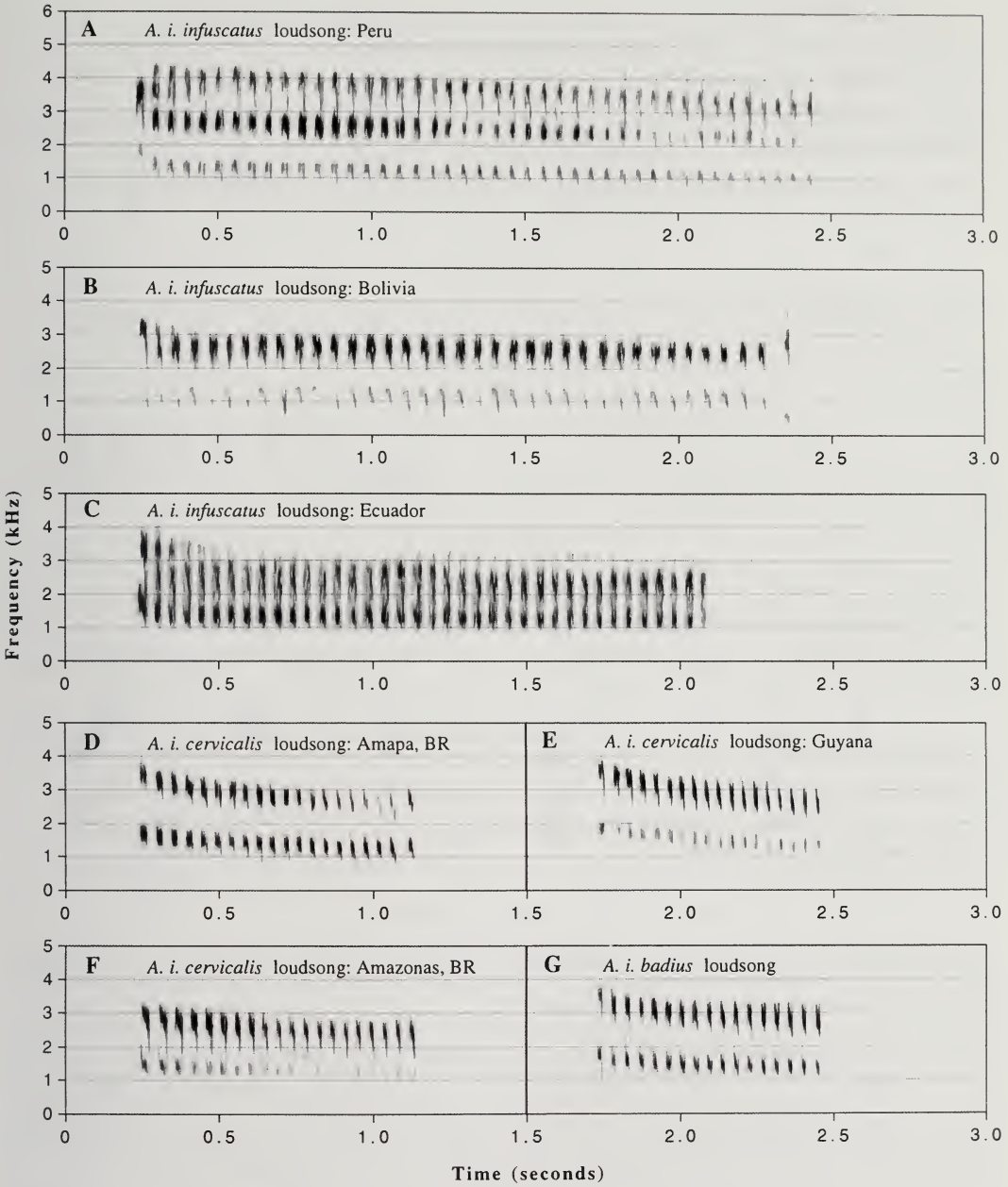

FIG. 4. Loudsongs of subspecies of *Automolus infuscatus*: (A) *A. i. infuscatus* from Loreto, Peru (T. A. Parker recording, LNS #29335); (B) *A. i. infuscatus* from Pando, Bolivia (T. A. Parker recording, LNS #38893); (C) *A. i. infuscatus* from Napo, Ecuador (K. J. Zimmer recording); (D) *A. i. cervicalis* from Amapá, Brazil (K. J. Zimmer recording); (E) *A. i. cervicalis* from Guyana (R. S. Ridgely recording); (F) *A. i. cervicalis* from Amazonas, Brazil (M. Cohn-Haft recording, LNS #48574); and (G) *A. i. badius* from Amazonas, Brazil (K. J. Zimmer recording).

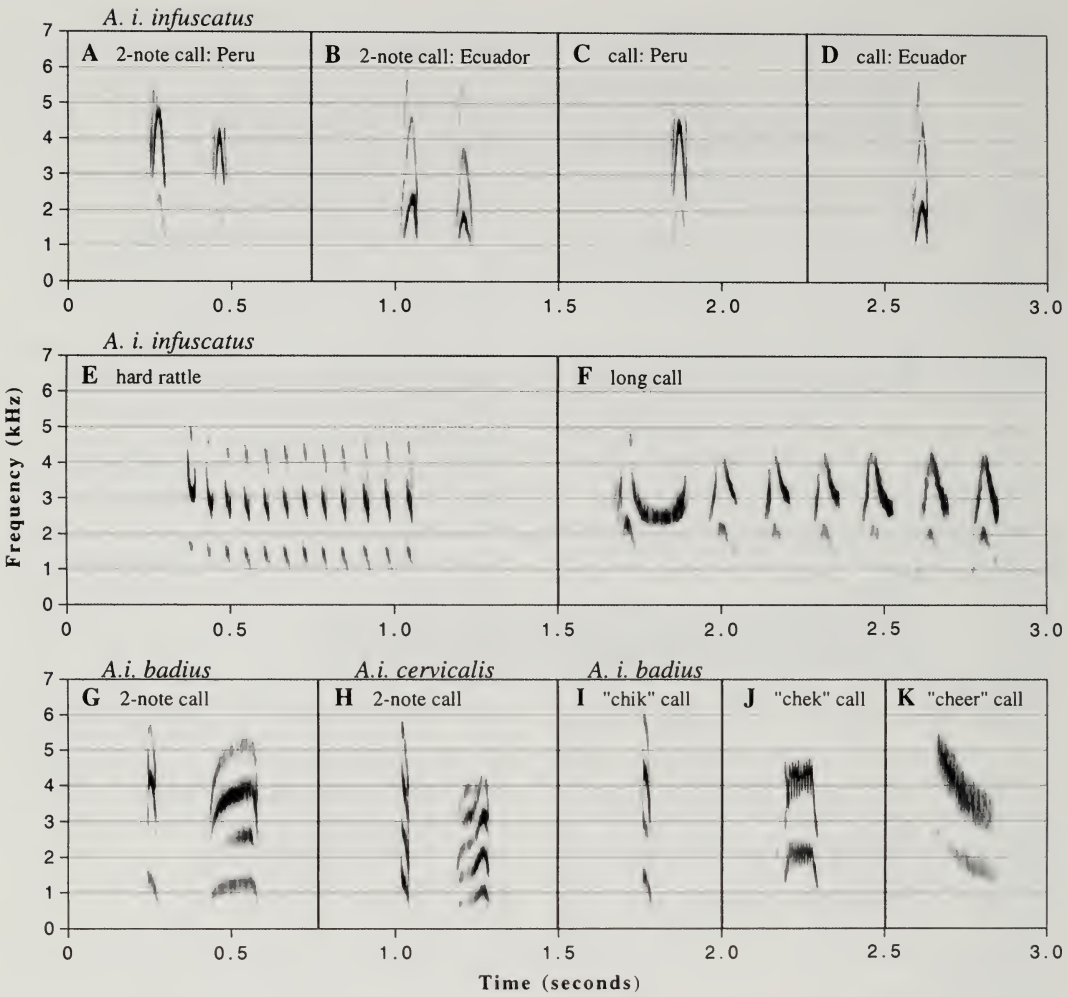

FIG. 5. Types of calls of subspecies of *Automolus infuscatus*: (A) two-note call of *A. i. infuscatus* from Madre de Dios, Peru (T. A. Parker recording, LNS #24224); (B) two-note call of *A. i. infuscatus* from Napo, Ecuador (K. J. Zimmer recording); (C) single-note call of *A. i. infuscatus* from Madre de Dios, Peru (T. A. Parker recording, LNS #23955); (D) single-note call of *A. i. infuscatus* from Napo, Ecuador (K. J. Zimmer recording); (E) hard rattle call of *A. i. infuscatus* from Madre de Dios, Peru (T. A. Parker recording, LNS #24123); (F) long call of *A. i. infuscatus* from Loreto, Peru (T. A. Parker recording, LNS #30724); (G) *chik-qwaah* call of *A. i. badius* from Amazonas, Brazil (K. J. Zimmer recording); (H) *chik-qwaah* call of *A. i. cervicalis* from Amazonas, Brazil (M. Cohn-Haft recording, LNS #48574); (I) *chik* call of *A. i. badius* from Amazonas, Brazil (K. J. Zimmer recording); (J) *chek* call of *A. i. badius* from Amazonas, Brazil (K. J. Zimmer recording); and (K) *cheer* call of *A. i. badius* from Amazonas, Brazil (K. J. Zimmer recording).

gleaners from south of the Amazon and east of the Rio Madeira (= *A. i. paraensis*) differ dramatically in their vocalizations from all other populations in the complex (Figs. 3–5). The loudsongs of *A. i. paraensis* differ in pattern, pace, pitch, tonal quality, and in individual note shape from the loudsongs of any other populations. Their calls (both single-noted and two-noted) and long calls are equally distinct from the corresponding vocalizations of any other subspecies.

The vocal distinctions between *A. i. paraensis* and other Olive-backed Foliage-gleaners are even more noteworthy when the lack of intrataxon variation within the complex is considered. Tape recordings of nominate *A. i. infuscatus* from Ecuador, Peru, and Bolivia show no striking geographic differences in

	paraensis	***infuscatus***	***purusianus***	***cervicalis***	***badius***
Size	Large	Large	Large	Small	Small
Back color	Dark brownish-olive	Dark brownish-olive	Hair brown	Dark brownish-olive	Raw Umber/ Prout's Brown
Crown/Nape color	Grayer than back	Same as back	Same as back	Warmer brown than back	Same as back
Crown scaling	Distinct	Indistinct	Indistinct	Indistinct	Indistinct
Color of breast/belly	Dingy gray-buff	Dingy gray-buff	Dingy gray-buff	Dingy gray-buff	Grayer than other taxa
Song type	2–17 widely spaced notes	Long, descending rattle (> 35 notes)	Unknown	Short, descending rattle (< 25 notes)	Short, descending rattle (< 25 notes)
Note structure	Strongly modulated	Unmodulated	Unknown	Unmodulated	Unmodulated
Note length	Long	Short	Unknown	Short	Short
Two-note calls	Notes mildly differentiated & liquid	Notes mildly differentiated & sharp	Unknown	Notes strongly differentiated	Notes strongly differentiated

FIG. 6. A summary of plumage, biometric, and vocal characters distinguishing the five subspecies in the Olive-backed Foliage-gleaner (*Automolus infuscatus*) group. Capitalized color descriptions follow Smithe (1975). Measurement data are provided in Table 1.

loudsongs or calls (Figs. 4, 5). Similarly, loudsongs of *A. i. cervicalis* do not vary from Manaus, Brazil to Amapá or Guyana, nor do they appear to differ from recordings of *A. i. badius* from west of the Rio Negro (Fig. 4).

Apart from the highly differentiated vocalizations of *A. i. paraensis*, there is further vocal variation within the complex to consider. The songs and calls of *A. i. infuscatus*, *A. i. badius*, and *A. i. cervicalis* all are far more similar to one another than any of them are to *A. i. paraensis*. However, the songs of the two north bank forms are only half as long as those of nominate *infuscatus* (Fig. 4), and at least some of the calls of both *A. i. badius* and *A. i. cervicalis* would appear to be diagnosably different as well (Fig. 5).

Morphological variation corresponds to some of the divisions suggested by vocal characters. Biometrically, the three southern forms (*A. i. infuscatus*, *A. i. purusianus*, and *A. i. paraensis*) are larger in most measured characters than are the two northern forms (*A. i. badius* and *A. i. cervicalis*). *Automolus i. badius* averaged smaller than each of the three southern forms in six of the eight characters measured. Similarly, *A. i. cervicalis* averaged smaller than *A. i. infuscatus* and *A. i. paraensis* in six characters, and differed from *A. i. purusianus* in seven characters. The three southern subspecies were poorly differentiated from one another biometrically. *Automolus i. infuscatus* and *A. i. paraensis* showed no differences over the eight mensural characters that I examined, and each differed from *A. i. purusianus* only in wing chord. The northern subspecies differed from one another in only three of the eight characters.

Plumage distinctions, although subtle, were consistent for each of the subspecies, and showed some trends that follow the north-south division in biometric differences. The smaller, northern subspecies were generally browner dorsally with only a slight dark scaling pattern to the crown and nape feathers. This was particularly true of *A. i. badius*, which was uniformly reddish-brown above. *Automolus i. cervicalis*, although more olivaceous on the back than *A. i. badius*, was still distinctly browner on the crown and nape than were the southern subspecies. This agrees with Hellmayr (1925:213), who stated that *A. i. cervicalis* was "similar to *A. i. infuscatus*, but crown and hindneck decidedly rufescent, more or less contrasting with olive brown of back, and flanks generally more brownish." Of the larger, southern subspecies, two (*A. i. infuscatus* and *A. i. paraensis*) were generally drab and more olivaceous dorsally, with a more pronounced pattern of dark scaling on the crown and nape. The contrasting gray crown and nape of *A. i. paraensis* were cited by Hartert (1902:61) in his description of the subspecies, and also were noted, along with the drabber coloration of the upperparts, by Hellmayr (1925:214) in his review of the complex.

The extremes of morphological variation within the complex are found in a comparison of *A. i. badius* (small; distinctly reddish-brown back; nape and crown concolor with the back; slight dark scaling to crown and nape; distinctly grayish underparts) and *A. i. paraensis* (large; back color olive; nape and crown contrastingly grayer than back; crown and nape feathers with distinctly scaly pattern; underparts dingy buff). These two forms are divergent enough that, in the absence of other populations, they could be considered specifically distinct on morphological grounds alone. However, unless vocal characters are considered, none of the other named subspecies is sufficiently different morphologically from both *A. i. badius* and *A. i. paraensis* to justify recognition of more than one species, at least under a biological species concept.

Spectrographic and auditory comparison of vocal characters throughout the genus suggests that *A. i. paraensis* may be more closely related to the subspecies of White-eyed Foliage-gleaner (*A. leucophthalamus*) in northeast Brazil (*A. l. lammi*), than it is to any other subspecies of *A. infuscatus*. The loudsongs of *A. i. paraensis* are more similar in pitch, pace, pattern, and note shape to those of *A. l. lammi* (Fig. 7A) than they are to those of any other member of the *A. infuscatus* complex. The loudsongs of *A. i. paraensis* and *A. l. lammi*, although different in several characters, are markedly similar to one another in their frequency-modulated, strident quality, a character that is not shared with any other taxon in the genus (KJZ recordings). The two-noted call of *A. l. lammi* (Fig. 7B) also is closer to that of *A. i. paraensis* than are the corresponding calls of nominate *A. infuscatus* (Fig. 5A,

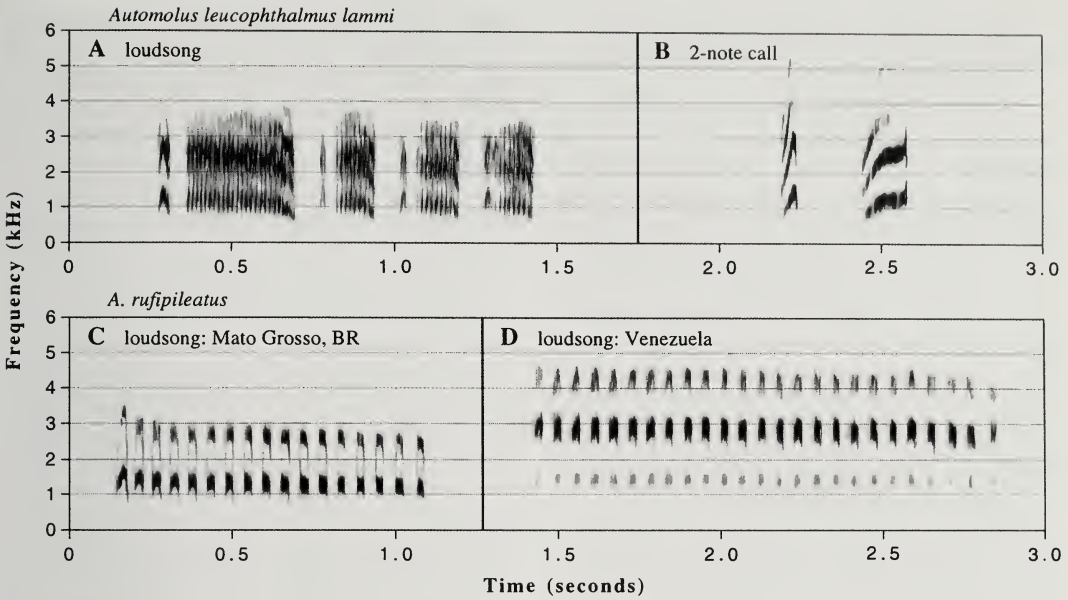

FIG. 7. (A) loudsong of *Automolus leucophthalamus lammi* from Sergipe, Brazil; (B) two-note call of *A. l. lammi* from Sergipe, Brazil; (C) loudsong of *A. rufipileatus* from Mato Grosso, Brazil; and (D) loudsong of *A. rufipileatus* from Bolívar, Venezuela (K. J. Zimmer recordings).

B). Willis (1988) suggested a possible superspecies relationship between *A. infuscatus* and *A. leucophthalamus* based on certain vocal similarities, but did not elaborate. On the basis of morphological characters, Vaurie (1980) also treated *A. infuscatus* and *A. leucophthalamus* as being more closely related to one another than to other members of the genus. However, it also should be noted that the same analysis of morphological characters (in the absence of vocal characters) led Vaurie (1980) to include *Automolus dorsalis* (now = *Anabazenops dorsalis*; Kratter and Parker 1997) in the same superspecies grouping with *A. infuscatus* and *A. leucophthalamus*. The relationship of *A. l. lammi* to other members of the *A. leucophthalamus* complex will be considered in a separate paper.

The distribution of *A. i. paraensis* as a species level taxon distinct from other members of the complex makes sense biogeographically. There is a well-documented pattern of species replacement within genera across both the Amazon and the Madeira (Haffer 1992). The distribution of *A. i. paraensis* overlaps three proposed centers of avian endemism as defined by Cracraft (1985): the Rondônia Center, delimited by the Rio Madeira and Rio Beni to the west, the Amazon to the north, the limit of tropical humid forest to the south, and the Rio Tapajós (in some cases, the Rio Xingú) to the east; the Pará Center, delimited by the Rio Tapajós to the west, the Amazon to the north, the limit of tropical humid forest to the south, and the Rio Tocantins to the east; and the Belém Center, which extends from the Rio Tocantins on the west, north to the Amazon, east to the Atlantic Coast, and south to the limit of the tropical humid forest. Numerous species of birds are endemic to all or part of the range occupied by *A. i. paraensis* (Cracraft 1985).

Recent studies of Neotropical suboscine passerines have revealed numerous cases of cryptic biodiversity, in which distinct species level taxa with dramatically different vocalizations were long overlooked because of their morphological similarity to more widespread forms (e.g., Pierpont and Fitzpatrick 1983; Willis 1992; Bierregaard et al. 1997; Zimmer and Whittaker 2000a, 2000b; Zimmer et al. 2001). As access to behavioral, ecological, vocal, and molecular data increases, it is becoming clear that taxonomies based solely on morphological distinctions severely underestimate

species level biodiversity. Olive-backed Foliage-gleaners provide yet another example.

TAXONOMIC CONCLUSIONS

Automolus infuscatus paraensis differs substantially in every known vocal character from all other subspecies in the complex. It also differs morphologically from all other members of the group, although these distinctions are more subtle. In particular, it can be separated from all other Olive-backed Foliage-gleaners by the contrasting grayish crown and nape, with broader, more contrasting dark fringes to the individual feathers. It is further differentiated from the two northern subspecies by its larger size, and lack of brown coloration on the crown or back.

The extent of the vocal differences alone is more than sufficient to support the recognition of *A. i. paraensis* as a separate species under any of the widely accepted species concepts (McKitrick and Zink 1988). Because *A. i. paraensis* is allopatrically or parapatrically distributed with respect to the other members of the complex, the most difficult species concept to satisfy is the biological species concept. A primary challenge in applying the biological species concept to allopatrically distributed taxa is the need to judge whether or not the taxa are sufficiently differentiated as to prevent extensive hybridization in the event of secondary contact. Johnson et al. (1999) advocated using the degree of differentiation shown between accepted biological species in the same genus as a yardstick for assessing whether a taxon has diverged sufficiently to be considered a separate species under the Biological Species Concept (BSC). The Chestnut-crowned Foliage-gleaner (*A. rufipileatus*) is broadly sympatric with all of the subspecies of Olive-backed Foliage-gleaners (Ridgely and Tudor 1994), and thus provides an appropriate yardstick for comparison of species level vocal divergence within the genus. Loudsongs of *A. rufipileatus* from north and south of the Amazon (Fig. 7C, D) are far more similar to those of all other members of the *A. infuscatus* complex, excluding *paraensis*, (Fig. 4) than are loudsongs of *A. i. paraensis*. Spectrographic and auditory comparison reveals that the vocal differences between *A. i. paraensis* and all other subspecies in the *Automolus infuscatus* complex are as great or greater than between those subspecies and any congener outside of the complex. This would suggest that the vocal differences alone present effective mechanisms for reproductive isolation between *A. i. paraensis* and any other member of the group.

The relationships of the other subspecies in the complex are less obvious. It is tempting to recognize the two northern subspecies, *A. i. badius* and *A. i. cervicalis*, as a species distinct from the more southern *A. i. infuscatus* and *A. i. purusianus*. The northern birds are distinctly smaller, and differ in certain plumage characters. More importantly, they differ in several vocal characters from nominate *A. infuscatus*, although the differences are less obvious than those found in *A. i. paraensis*. The two groups (northern versus southern) would certainly meet phylogenetic species concept (PSC) criteria for diagnosability as separate species, and they may ultimately prove to be distinct biological species as well. However, I believe that vocal differences among these groups are subtle enough to warrant a more rigorous quantitative vocal analysis, and current sample sizes of the recording inventories for both *A. i. badius* (n = 3) and *A. i. cervicalis* (n = 8, but most recordings are of loudsongs without calls) are inadequate. Furthermore, it cannot be assumed that *A. i. purusianus*, for which there are no definite tape recordings, belongs with nominate *A. infuscatus*, solely because of morphological similarity. In the absence of any data on the vocalizations of *A. i. purusianus*, and lacking sufficient vocal samples of *A. i. badius* and *A. i. cervicalis*, I follow the conservative path of maintaining these forms, along with nominate *A. i. infuscatus*, as part of the *Automolus infuscatus* complex. I propose that the complex consists of two biological species as follows:

Automolus infuscatus Sclater—Olive-backed Foliage-gleaner
- *A. i. infuscatus* Sclater
- *A. i. cervicalis* Sclater
- *A. i. badius* Zimmer
- *A. i. purusianus* Todd

Automolus paraensis Hartert—Pará Foliage-gleaner

The English name chosen for *A. paraensis* highlights the Brazilian state which encompasses the bulk of its range, and from which

the majority of specimens, including the type, have been collected. I have chosen to retain "Olive-backed Foliage-gleaner" as the English name for all other members of the complex. Should the two northern taxa prove to be specifically distinct from the two southern taxa, then the prefix "Olive-backed" would most appropriately be applied to the southern birds.

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APPENDIX 1

Recording locations and recordists. Numbers following each name represent the number of individual birds recorded by the recordist at each site.

A. i. paraensis.—BRAZIL: Alta Floresta region, Mato Grosso (K. J. Zimmer 20); Caxiuanã Forest Reserve, Pará (K. J. Zimmer 9); Cachoeira Nazaré, Rondônia (T. S. Schulenberg 1).

A. i. infuscatus.—BOLIVIA: Suarez, Pando (T. A. Parker 1). ECUADOR: La Selva Lodge, N bank Rio Napo, Napo (R. A. Behrstock 2, G. H. Rosenberg 1); Santiago, Morona-Santiago (M. B. Robbins 2); Tiputini Biodiversity Station, S bank Rio Napo, Napo (K. J. Zimmer 9). PERU: S bank Rio Napo, 80 km N of Iquitos, Loreto (T. A. Parker 2, G. H. Rosenberg 1); Quebrada Sucusari, N bank Rio Napo, Loreto (T. A. Parker 6); Yanamono, N bank Rio Napo, Loreto (G. H. Rosenberg 2); Cocha Cashu, Manu National Park, Madre de Dios (T. A. Parker 1); Tambopata Reserve, Madre de Dios (M. L. Isler 1, L. Kibler 3, M. Palmer 2, T. A. Parker 16, G. A. Rosenberg 1, A. Van den Berg 4, K. J. Zimmer 1).

A. i. cervicalis.—BRAZIL: Serra do Navio, Amapá (K. J. Zimmer 1); left bank Rio Negro north of Manaus, Amazonas (M. Cohn-Haft 1, A. Whittaker 1). GUYANA: Baramita (M. B. Robbins 1); Iwokrama Reserve (R. S. Ridgely 1, M. B. Robbins 2); Waruma River (M. B. Robbins 1).

A. i. badius.—BRAZIL: São Gabriel da Cachoeira, Amazonas (right bank Rio Negro) (K. J. Zimmer 3).

A. i. purusianus or A. i. infuscatus.—BRAZIL: Porongaba, Acre (A. Whittaker 2).

APPENDIX 2

List of localities and lending institutions for specimens examined. All specimens were from the following institutions: Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania (ANSP); Carnegie Museum, Pittsburgh, Pennsylvania (CM); Field Museum of Natural History, Chicago, Illinois (FMNH); Los Angeles County Museum, Los Angeles, California (LACM); Louisiana State Univ. Museum of Natural Science, Baton Rouge, Louisiana (LSUMZ); National Museum of Natural History, Washington, D.C. (USNM); and the Yale Peabody Museum of Natural History, New Haven, Connecticut (YPM).

A. i. paraensis (46 males, 31 females, 5 sex unknown).—BRAZIL: Bela Vista, Pará (CM, 1 female); Belém, Pará (FMNH, 1 female; USNM, 10 males, 7 females, 5 sex unknown); Belém-Brasilia Rd. Km 75–107, Pará (LACM, 8 males, 2 females; LSUMZ, 3 males); Benevides, Pará (CM, 4 males, 4 females; YPM, 2 males, 1 female); Benfica, Pará (FMNH, 1 female); Cachoeira Nazaré, Rondônia (FMNH, 1 male); Colônia do Mojuy, Pará (CM, 8 males, 2 females; FMNH, 1 male, 1 female; YPM, 1 male); Lago do Araipa, Pará (LACM, 3 females); Mirituba, Pará

(CM, 2 males, 3 females; YPM, 1 male, 1 female); Pedra Branca, Rio Anari, Rondônia (FMNH, 2 males, 1 female); Santarém, Pará (CM, 2 males, 2 females; YPM, 1 female); Utinga, Pará (USNM, 1 male).

A. i. infuscatus (50 males, 33 females).—BOLIVIA: Cojiba, 12–20 km SW, Pando (LSUMZ, 6 males, 6 females). COLOMBIA: Caño Yerly, Meta (FMNH, 1 male); Guamués, Estación de Bombeo, Putamayo (FMNH, 1 male); San Antonio, Putamayo (FMNH, 2 males, 1 female). ECUADOR: Limoncocha, Napo (LSUMZ, 3 males, 2 females); Sucumbios Province (ANSP, 3 males, 2 females); Taisha, Morona-Santiago (ANSP, 3 males, 2 females); Zancudo Cocha, Napo (ANSP, 1 male, 2 females). PERU: Calientillo, Loreto (FMNH, 2 females); Ccollpa, Río Tambopata, Madre de Dios (FMNH, 1 male); Cordillera de Pantiacolla, E slope at base, Madre de Dios (FMNH, 1 female); Cordillera de Pantiacolla, E slope near summit, Madre de Dios (FMNH, 1 female); Iquitos, S bank 40 mi. E, Loreto (FMNH, 2 males, 1 female); Libertad, 1.5 km S, Loreto (LSUMZ, 4 males, 2 females); Puerto Arturo, Loreto (FMNH, 1 female); Puerto Bermudez, Pasco (FMNH, 1 male); Puerto Maldonado, 105–110 km on road to Quincemil (LSUMZ, 4 males, 2 females); Puerto Yessup, Pasco (ANSP, 5 males); Quebrada Sucusari, Loreto (LSUMZ, 2 males, 3 females); Refugio Juliaca, Madre de Dios (LSUMZ, 3 males); Río Colorado, mouth, Madre de Dios (FMNH, 1 male); Río Manití, Loreto (ANSP, 1 male); Río Shesha, Ucayali (LSUMZ, 3 males, 3 females); Río Yanayacu, Loreto (LSUMZ, 3 males, 2 females).

A. i. purusianus (28 males, 12 females).—BRAZIL: Arimã, Amazonas (CM, 2 males; FMNH, 1 male); Caviana, opposite Manacapuru, Amazonas (CM, 2 males, 2 females; YPM, 1 male, 1 female); Huitanaã, Amazonas (CM, 5 males, 4 females; FMNH, 1 male; YPM, 2 males, 1 female); Nova Olinda, Amazonas (CM, 2 males; YPM, 1 male); São Paulo de Olivença, Amazonas (CM, 7 males, 2 females; YPM, 2 males, 1 female); Tonantins, S bank Solimães, Amazonas (YPM, 2 males, 1 female).

A. i. cervicalis (25 males, 13 females, 1 sex unknown).—BRAZIL: BV-8, 6 mi E on Venezuela border, Roraima (FMNH, 1 male); Mazagão, Amapá (LACM, 1 male); Mucajai River S of Boa Vista, Roraima (LACM, 1 male); Obidos, Pará (CM, 2 males, 2 females); Porto Platon, Amapá (USNM; 1 male, 1 female); Rio Aracauá, Amapá (CM, 2 males, 1 female; YPM, 1 male); Serra do Navio, Amapá (FMNH, 1 female; USNM, 5 males, 2 females); Sorocaima, Roraima (FMNH, 2 males). FRENCH GUIANA: Mana River, Fleuve (CM, 4 males, 3 females); Tamanoir, Saut (CM, 2 males, 1 female; YPM, 1 male, 1 female). GUYANA: Boundary Camp, Acarai Mountains (FMNH, 1 male). SURINAME: Kayser Gebergte Airstrip (FMNH, 1 sex unknown); Neger Kreek (YPM, 1 female); Wilhelmina Mountains, West River (FMNH, 1 male).

A. i. badius (38 males, 18 females, 1 sex unknown).—BRAZIL: Maluracá, Canal at mouth, Amazonas (USNM, 2 males); Membeca, Amazonas (CM, 10 males, 7 females); Panela de Onça, Cachoeira, Amazonas (USNM, 1 male); São Gabriel da Cachoeira, Amazonas (USNM, 2 males, 1 female); Serra Imeri, Amazonas (ANSP, 1 male; USNM, 3 males); Tonantins, Amazonas (CM, 9 males, 3 females). COLOMBIA: San Felipe, Guainía (USNM, 1 male). VENEZUELA: Caño Caripo, Amazonas (USNM, 1 female); Cerro Duida, Amazonas (USNM, 1 female); Cerro de la Neblina, Amazonas (FMNH, 2 males, 1 female); Cerro Marahuaca, Amazonas (USNM, 1 female); Cerro Yapacana, Amazonas (USNM, 1 male, 1 female, 1 sex unknown); Río Caura, Bolívar (CM, 4 males, 1 female); Río Vaciva, below mouth of, Amazonas (USNM, 1 male); Río Yatúa, upper Amazonas (USNM, 1 male); San Carlos de Río Negro, Amazonas (FMNH, 1 female).

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REDEFINING RANGE OVERLAP BETWEEN THE SHARP-TAILED SPARROWS OF COASTAL NEW ENGLAND

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ABSTRACT.—With the designation of Nelson's Sharp-tailed Sparrow (*Ammodramus nelsoni*) and Saltmarsh Sharp-tailed Sparrow (*A. caudacutus*) as species of high conservation priority in the northeastern United States, the need to document fully their abundance, distribution, and the extent of range overlap has become increasingly important. We surveyed saltmarshes in coastal New England for both species from 1997 to 2000. The current overlap zone extends from Parker River, Massachusetts, north to Weskeag River, Maine, which expands the previously reported range overlap of 48 km to 208 km. Among the 49 sites surveyed within the current overlap zone, both species were present at 25 sites. It is possible that the species have experienced range expansion over the last several decades, especially the Nelson's Sharp-tailed Sparrow. Our findings indicate that the nominate subspecies of the Saltmarsh Sharp-tailed Sparrow warrants the greatest conservation concern given its limited geographic range, a potentially expanding hybrid zone with *A. n. subvirgatus*, and the potential for habitat degradation from an oil spill associated with the urban/industrial centers of the Northeast. *Received 24 May 2001, accepted 3 February 2002.*

In 1995, the American Ornithologists' Union Committee on Classification and Nomenclature split the Sharp-tailed Sparrow (then *Ammodramus caudacutus*) into two species: the Saltmarsh Sharp-tailed Sparrow (*A. caudacutus*) in the south and the Nelson's Sharp-tailed Sparrow (*A. nelsoni*) in the north (American Ornithologists' Union 1995). This decision followed closely the recommendations of Greenlaw (1993) who reported differences in song, morphology, and habitat, with interbreeding limited to an overlap zone of approximately 48 km on the Maine coast (American Ornithologists' Union 1998). Differences in habitat seem to result from the use of inland fresh and brackish marshes as well as saltmarsh habitat by Nelson's Sharp-tailed Sparrows, and the nearly exclusive use of saltmarshes by Saltmarsh Sharp-tailed Sparrows (Erskine 1992, Greenlaw and Rising 1994). Furthermore, the coastal physiography in the southern Gulf of Maine varies from larger marshes in the south to smaller, widely scattered marshes in the northeast (Fefer and Shettig 1980). This pattern in coastal features corresponds roughly to the recognized range boundaries of each species in Maine. In New England, however, the extent of overlap between the nominate subspecies of Saltmarsh Sharp-tailed Sparrow (*A. c. caudacutus*) and the maritime subspecies of Nelson's Sharp-tailed Sparrow (*A. n. subvirgatus*) is not well known.

For more than a century, ornithologists have reported on the range boundaries of the *caudacutus* and *subvirgatus* populations of sharp-tailed sparrows in coastal Maine (Norton 1897; Montagna 1940, 1942; Palmer 1949; Greenlaw 1993). As early as 1940, Montagna (1940) discussed sites where *caudacutus* and *subvirgatus* co-occurred during the breeding season. Later, Greenlaw (1993) described a zone of overlap among the subspecies from Scarborough Marsh in Cumberland County, Maine, north to Popham Beach in Phippsburg, Sagadahoc County, Maine, where limited interbreeding appeared to be taking place (Greenlaw 1993, Rising and Avise 1993). However, since 1996, Nelson's Sharp-tailed Sparrows have been reported during the breeding season south of this zone in Biddeford, York County, Maine (Brinker 1997) and at Great Bay National Wildlife Refuge, New Hampshire (G. Taylor pers. comm.). These observations, together with limited

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DNA evidence from Massachusetts (Rising and Avise 1993), raise doubts concerning the southern boundary and suggest possible expansion of the overlap zone. Prior to our study, the understanding of the distribution of sharp-tailed sparrows in coastal New England was based on skilled but intermittent observations, rather than systematic surveys. Greenlaw and Rising (1994) indicated that both local and regional surveys would document conclusively the extent of overlap between these species and would constitute a positive step toward appropriate management.

The Saltmarsh Sharp-tailed Sparrow and the *subvirgatus* race of the Nelson's Sharp-tailed Sparrow are of high conservation priority in the northeastern United States according to the Partners in Flight prioritization system (Carter et al. 2000) because large proportions of their global populations breed there (>90% for Saltmarsh Sharp-tailed Sparrow). Efforts in the U.S. to conserve these species are hampered by a lack of data regarding their distribution, abundance, and population trends, and by uncertainty over which states or agencies have jurisdiction over significant populations. As a first step in evaluating the status of these two sparrows and to provide a baseline from which to monitor population trends and future shifts in range boundaries, we examined the extent and species composition of this contact zone among saltmarshes in coastal New England.

STUDY AREA AND METHODS

We documented the distribution and abundance of both species of sharp-tailed sparrows along the Atlantic coast from Greenwich, Connecticut, to Lubec, Maine. We surveyed most marshes in coastal New England, but excluded small (<5 ha) marshes and patches of fringing marsh along rivers and sheltered bays. We established fixed points in each marsh and distributed them throughout the wetland as feasible given difficulties of traversing marshes (i.e., points were neither along transects nor randomly located). We positioned each point ≥250 m from all other points and ≥50 m from any upland edge. We marked each point with a 0.5-m stake flag inscribed with a unique identification number to facilitate revisiting the exact location. We identified each species by either sight or sound and counted the number of individuals of each species ≤100 m from each point during a 10-min count period. We visited most points on three occasions during the breeding season, from early June through mid-August, 1997–2000, except when prevented by extreme tidal flooding or when the point was discontinued due to frequent listening difficulties (e.g., traffic noise) or other logistical constraints. We allowed approximately two weeks to elapse between visits to an individual point. We used two indices to express relative abundance of each species at a given site: the maximum number of individuals detected ≤100 m from a point and the percentage of points within each site where each species was present.

RESULTS

We surveyed 244 marshes from Maine to Connecticut with 911 total points visited. We detected Saltmarsh Sharp-tailed Sparrows at 132 (54%) marshes: 44 (58%) in Connecticut, 30 (86%) in Rhode Island, 29 (51%) in Massachusetts, three (75%) in New Hampshire, and 26 (36%) in Maine. We documented Saltmarsh Sharp-tailed Sparrows at six sites north of its published northern range limit: Popham Beach, Maine (Greenlaw 1993, American Ornithologists' Union 1995), extending this species' documented range northeastward about 65 km (Fig. 1, Table 1). Based on our survey, the northernmost site for this species was the Weskeag River estuary in South Thomaston, Knox County, Maine. We did not detect Saltmarsh Sharp-tailed Sparrows at any of the 30 marshes surveyed north of this site to Lubec, Maine, on the Canadian border.

We encountered Nelson's Sharp-tailed Sparrows at 54 sites from Lubec, Maine, to Parker River National Wildlife Refuge, Massachusetts. This included 13 occupied sites south of the former range boundary, indicating a southward range extension of approximately 95 km (Fig. 1, Table 1). We did not detect Nelson's Sharp-tailed Sparrows at 165 marshes from Parker River south to Greenwich, Connecticut.

Range boundaries were not abrupt for either species. Instead, the percentage of points with each species present (an index to abundance) declined gradually at marshes near the edge of each species' geographic range (Table 1). Among the 11 sites surveyed within the former overlap zone, seven marshes (64%) were occupied by both species and one marsh (9%) by only Nelson's Sharp-tailed Sparrows. We did not detect sharp-tailed sparrows of either species at any of the three (27%) remaining marshes. Within the current overlap zone of 49 sites, we found at least one species at 35 sites (71%), both species at 25 sites (51%), and neither species at 14 sites (29%; Table 1).

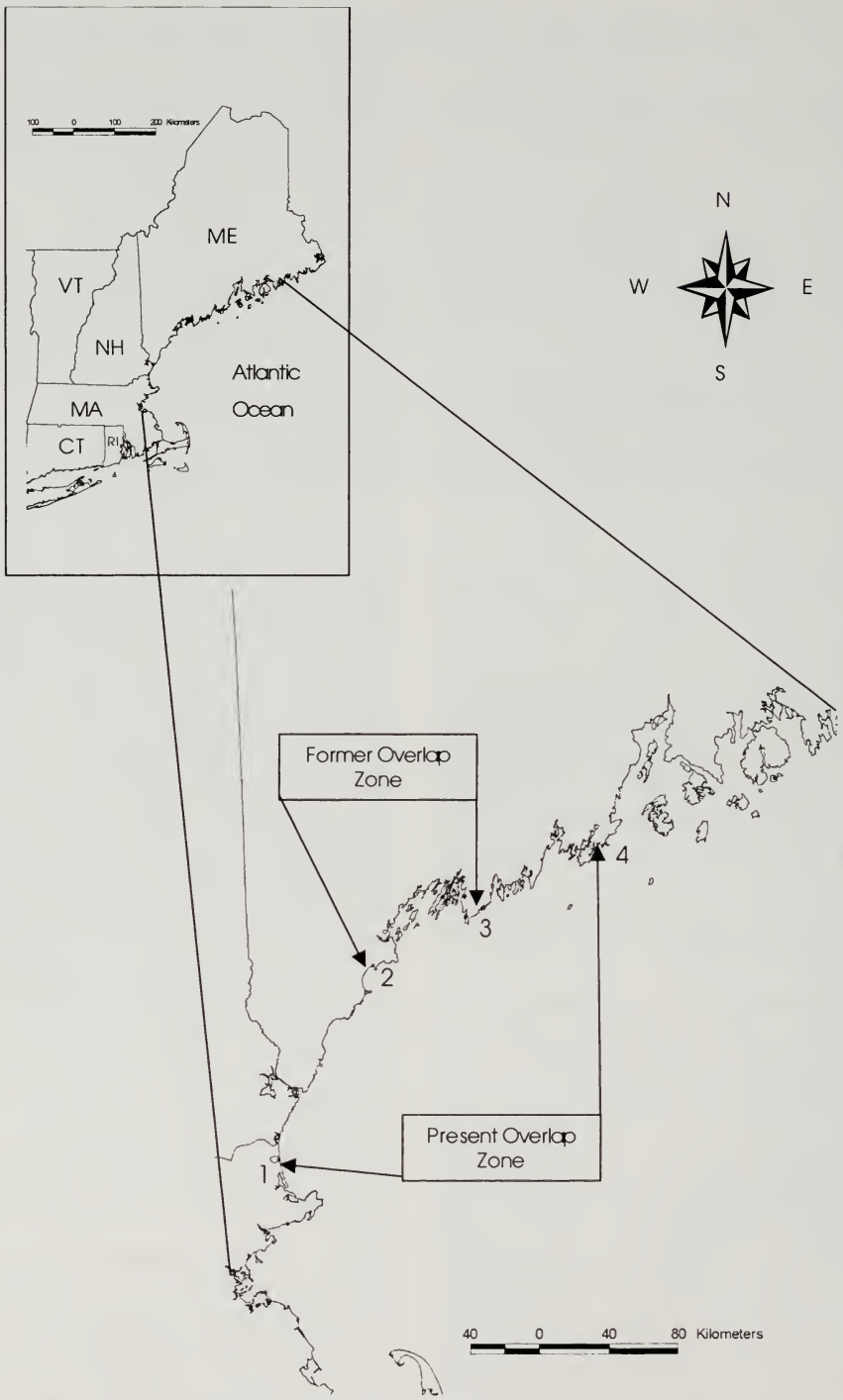

FIG. 1. Range overlap of Saltmarsh Sharp-tailed Sparrow and Nelson's Sharp-tailed Sparrow in coastal New England, based on point counts conducted June through August, 1997–2000. Numbers correspond to sites discussed in text: (1) Parker River, (2) Scarborough Marsh, (3) Popham Beach, (4) Weskeag River.

TABLE 1. Indices of abundance of Nelson's and Saltmarsh sharp-tailed sparrows among 49 saltmarshes in coastal New England, based on 10-min, 100-m radius point counts conducted June through August, 1997–2000. Sites are arranged from north to south. Names in bold are sites within the previously known overlap zone. Saltmarsh Sharp-tailed Sparrows were not detected at 30 marshes north of Weskeag River, Maine, and Nelson's Sharp-tailed Sparrows were not detected at 165 marshes south of Parker River, Massachusetts.

State	Site	Number of points	Maximum number of individuals per point		Percentage of points with species present	
			Nelson's	Saltmarsh	Nelson's	Saltmarsh
Maine	Weskeag River[a]	20	7	5	90	60
	Friendship	2	0	0	0	0
	Havener Cove[b]	1	0	0	0	0
	Meetinghouse Cove[b]	3	0	0	0	0
	Western Branch[b]	2	0	0	0	0
	Broad Cove South[b]	2	0	0	0	0
	Greenland Cove[b]	1	0	0	0	0
	Deer Meadow Brook	10	4	2	80	10
	Dyer River	9	14	6	89	33
	Maine Yankee	2	0	0	0	0
	Chewonki Creek	2	0	0	0	0
	Montsweag Brook	4	0	0	0	0
	Reid State Park	6	6	1	83	50
	Little Riv. (Georgetown)	10	6	3	100	50
	West Georgetown	2	1	0	50	0
	Newtown/Minot Creeks	10	5	2	90	50
	Popham Beach	10	9	3	90	50
	Sprague River[a]	12	8	4	75	25
	Small Point	3	0	0	0	0
	Mare Brook	5	11	7	100	80
	Maquoit Bay	6	4	1	83	17
	East Harspwell	2	0	0	0	0
	Cousins River	10	3	2	80	40
	Presumpscot River	4	3	0	25	0
	Fore River	2	0	0	0	0
	Spurwink River[a]	24	7	5	50	50
	Scarborough Marsh[a]	76	10	8	82	74
	Goosefare Brook	4	5	8	100	100
	Saco River	4	1	0	25	0
	Biddeford Pool	7	2	2	57	71
	Little River (Biddeford)	5	4	6	40	100
	Batson River[a]	12	5	6	58	50
	Sampson Cove[a]	3	0	1	0	33
	Kennebunk River	3	4	2	66	33
	Mousam River	5	0	1	0	20
	Little River (Wells)	5	1	1	20	60
	Webhannet River	36	4	12	47	58
	Ogunquit River[a]	19	8	7	74	58
	Upper York River[a]	10	2	6	60	50
	York River Tributaries[c]	3	0	0	0	0
	Braveboat Harbor[a]	12	0	1	0	8
	Crescent Surf	3	0	3	0	100
New Hampshire	Hampton River	18	0	3	0	39
	Little River (Hampton)	4	0	0	0	0
	Luberland Creek	2	0	9	0	100
	Chapman's Landing	5	6	3	60	100
Massachusetts	Blackwater River	10	2	12	40	90
	Salisbury Beach	2	0	4	0	50
	Parker River[a]	40	1	10	3	78

[a] Surveyed for two breeding seasons.
[b] Small sites along the Medomak River.
[c] Dolly Gordon Brook, Cider Hill Creek, and Boulter Pond Brook.

DISCUSSION

We think our measure of the overlap in distribution of these two species is accurate because we detected Saltmarsh Sharp-tailed Sparrows at the northernmost occupied site (Weskeag River) during every year visited (1997, 1998, and 2000), yet failed to detect them at the next site to the north (Mendall Marsh) during both 1998 and 1999 (not visited in 1997 or 2000). Furthermore, given the number of sites occupied by Saltmarsh Sharp-tailed Sparrows north of Popham Beach (n = 6) and similarly for Nelson's Sharp-tailed Sparrows south of Scarborough Marsh (n = 13), and the abundance of individuals of both species on specific point counts (Table 1), each species appears well established outside the former overlap zone.

The distribution of saltmarshes in coastal New England is not uniform and may influence the range boundaries of these sparrows. Marshes within the Gulf of Maine differ greatly in size, shape, and proximity from one another, with large expansive marshes shifting to small isolated marshes with increasing latitude (Fefer and Shettig 1980). Montagna (1942) and Palmer (1949) implied that this transition from large to smaller marshes has influenced the distribution of sharp-tailed sparrows. Furthermore, the ecological differences imposed by small, scattered marshes, which predominate in northeastern coastal Maine, in contrast to the large, nearly contiguous marshes found in southern New England, are likely to affect these species differently.

Habitat availability probably is not the primary determinant of the southern boundary for Nelson's Sharp-tailed Sparrows, because the southern terminus occurs in Massachusetts amid several large marshes in close proximity to one another. Instead, competition or some other environmental factor may be dictating the southern extent of Nelson's Sharp-tailed Sparrow. It is noteworthy that this southern boundary occurs at the northern extent of the congener, and possible ancestor, the Seaside Sparrow (*A. maritimus*; Zink and Avise 1990). Post and Greenlaw (1994) described aggressive interactions between sharp-tailed and Seaside sparrows where the latter often evicts sharp-tailed sparrows from territories and dominate interactions in feeding areas outside of territories. Such interspecific competition may contribute to the southern range extent of Nelson's Sharp-tailed Sparrow. Furthermore, with such limited foliage height diversity in the high marsh, perhaps there is only enough niche space for two ecologically similar species, although Nelson's Sharp-tailed Sparrows apparently breed successfully within the narrow marsh/upland interface at sites with great tidal range in the Bay of Fundy.

For the Saltmarsh Sharp-tailed Sparrow, however, habitat may be more important in defining its northern range limit. This species appears to use brackish (and certainly fresh) marshes less than Nelson's Sharp-tailed Sparrow (Greenlaw and Rising 1994), and the marsh along the Weskeag River is the last "true" saltmarsh with >150 ha of emergent marsh habitat for over 100 km northeast along the Maine coast. Penobscot Bay, an area which contains few marshes and little *Spartina*-dominated habitat, reaches its southwestern extreme <10 km from the mouth of the Weskeag River. Penobscot Bay may represent a barrier to effective colonization of the few larger marshes to the northeast.

Our data document the presence of each species outside previously accepted range boundaries and seem to indicate an expansion by both species. However, it also is possible that these species may have been present, but undetected for decades by birders. This is not unlikely for Saltmarsh Sharp-tailed Sparrows, given their faint "complex whisper song" and lack of an obvious flight display (Greenlaw 1993). This species could have been overlooked for decades in marshes north of Popham Beach. Less likely, however, is the failure to detect Nelson's Sharp-tailed Sparrows at sites south of Scarborough Marsh, given the large number of skilled observers and the sparrow's more obvious flight display and primary song (Greenlaw 1993).

Further monitoring is needed to determine whether the ranges of each species currently are expanding. The implications of two potentially expanding populations with a broadening hybrid zone may place increasing emphasis on the conservation of *A. c. caudacutus*, whose habitat use is inextricably linked with tidal marshes and whose range (outside the overlap zone) extends only from Massachusetts to New Jersey. Furthermore, catastrophic

events such as a large oil spill in this area of dense human population or a rise in sea level could greatly affect global population size of both species, but especially *A. c. caudacutus*.

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CONSERVATION STATUS OF THE BUFF-BREASTED SANDPIPER: HISTORIC AND CONTEMPORARY DISTRIBUTION AND ABUNDANCE IN SOUTH AMERICA

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ABSTRACT.—We present historic and contemporary information on the distribution and abundance of Buff-breasted Sandpipers (*Tryngites subruficollis*) in South America. Historic information was collated from the literature, area ornithologists, and museums, whereas contemporary data were derived from surveys conducted throughout the main wintering range in Argentina, Uruguay, and Brazil during the austral summers of 1999 and 2001. Variable circular plot sampling was used to estimate population densities. During 1999, the highest concentration of Buff-breasted Sandpipers in Argentina was in southern Bahía Samborombón (General Lavalle District) and areas north of Mar Chiquita coastal lagoon. During 2001, the highest concentrations in Brazil were at Ilha da Torotama and Lagoa do Peixe National Park. During 1999 and 2001, the highest concentrations of Buff-breasted Sandpipers in Uruguay were found along three lagoons (Laguna de Rocha, Laguna de Castillos, and Laguna Garzón) bordering the Atlantic Ocean. Population densities (birds/ha) of Buff-breasted Sandpipers were 0.11 (95% C.I. = 0.04–0.31) in Argentina, 1.62 (0.67–3.93) in Brazil, and 1.08 (0.37–3.18) in Uruguay. High turnover rates at survey sites, due to the formation of large, mobile flocks, contributed to moderately large confidence intervals around our population density estimates. Nevertheless, compared with historic accounts of Buff-breasted Sandpipers, our survey data indicate the population size of this species has declined substantially since the late 1800s and contemporary information suggests the species has continued to decline during the past three decades. Buff-breasted Sandpipers were found almost exclusively in pasturelands and appear to depend heavily upon intensive grazing by livestock, which maintain suitable short grass conditions. We discuss the need for protection of critical areas and proper range management to ensure appropriate habitat remains available for the species, and provide suggestions for future research needs. *Received 12 March 2001, accepted 31 January 2002.*

Buff-breasted Sandpipers (*Tryngites subruficollis*) probably numbered in the hundreds of thousands at the turn of the Twentieth Century (Forbush 1912, Hudson 1920). Long term shorebird surveys in central and eastern Canada indicate that the population size may be as low as 15,000 today (Brown et al. 2001, Morrison et al. 2001). This decline is attributed to commercial hunting during the late 1800s and early 1900s during the species' migration across the central United States and to a lesser degree on the wintering grounds in South America (McIlhenny 1943, Myers 1980, Canevari and Blanco 1994). A further negative effect on the population occurred during the widespread conversion of short grass prairies to agriculture in the U.S. plains (Wetmore 1927, Lanctot and Laredo 1994). In 1999, the Buff-breasted Sandpiper was proposed and then included in Appendix I of the

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Convention on the Conservation of Migratory Species of Wild Animals—United Nations Environmental Program (1999). The species also is ranked as one of high concern in the U.S. (Brown et al. 2001) and Canadian (Donaldson et al. 2000) shorebird conservation plans. These certifications encourage the study, management, and conservation of the species.

Within this framework, we conducted the first population wide survey of the species. The natural history of the Buff-breasted Sandpiper required that such a survey be conducted on the wintering grounds. During the breeding season, individuals occur sporadically and in unpredictable numbers throughout the high Arctic (Troy and Wickliffe 1990, Lanctot and Laredo 1994, Lanctot and Weatherhead 1997). Similarly, Buff-breasted Sandpipers are broadly dispersed and are unpredictable in distribution during spring and fall migration in the central plains of the U.S. and Canada (Skagen 1997; J. G. Strauch, Jr. unpubl. data). In contrast, Buff-breasted Sandpipers winter in a relatively small region of Argentina, Uruguay, and Brazil (Belton 1994, Blanco et al. 1993, Lanctot and Laredo 1994). Here, they are restricted to coastal areas that provide a sanctuary for the species because flooding and soil salinity limit agricultural development and promote cattle grazing (Soriano 1991). Buff-breasted Sandpipers, in turn, benefit from cattle grazing because of their dependence upon short grass pastures for winter habitat.

Here we present historical and contemporary information on the abundance and distribution of Buff-breasted Sandpipers in South America. Next, we document the abundance and locations where Buff-breasted Sandpipers were seen during systematic surveys in Argentina, Uruguay, and Brazil during the austral summers of 1999 and 2001. Then, we discuss the need for protection of critical areas and proper range management to ensure appropriate habitat remains available for the species. Finally, we recommend future research needs for the conservation of the species.

METHODS

Wintering and migration range.—We delineated the potential wintering range of Buff-breasted Sandpipers by plotting the locations of historic species records onto base maps with ArcView GIS software (Environmental Systems Research Institute, Inc. 1992). Information was obtained from published and grey literature, by local contacts and ornithology list servers, and from museums. When geographic coordinates for a location were not provided in the primary source of information (person or reference), we found locations and determined coordinates from ornithological gazetteers available for each country. We also used the spelling of place names in the gazetteers when available. We defined the main wintering and migration range of the species based on the distribution and timing of these observations, previous knowledge of the species' habitat use (Blanco et al. 1993), and the distribution of habitat types in the Río de La Plata Grasslands (see maps in León et al. 1984, Soriano 1991). The main wintering range encompassed the area where Buff-breasted Sandpipers were observed frequently and in large numbers during austral summer months (November through February), and where there were large patches of suitable habitat. Buff-breasted Sandpipers occasionally occur outside this area during winter although suitable habitat is patchily distributed and scarce (due to agriculture and urban development), making sightings unpredictable and infrequent. The migration range spanned the area where sightings were recorded during austral spring (August through October) and fall migration (March through May), or areas visited only occasionally by the species. Although only historic observations were used to delineate the migration and wintering areas, we included more recent observations in our tables and figures as they provided additional contemporary information on the species. Historic observations where the month of the sighting was missing (7 of 133 localities) were not used to delineate winter and migration boundaries.

Survey design and protocol.—We conducted surveys during early December, 1999, in Argentina and Uruguay. After learning that Buff-breasted Sandpipers also were using portions of Brazil, we initiated a second year of surveys in early December 2001. These surveys were limited to only Uruguay and Brazil because funds were limited.

Because all the available literature indicated Buff-breasted Sandpipers used land with short vegetation, we focused our surveys on short-vegetated areas such as intensively grazed pastures and newly established agricultural fields (e.g., rice fields). Here, pastures typically refer to native grass areas or old agricultural fields with crop residue that are being grazed. Tall grass, tall emergent areas of marshes, and forested areas were avoided. Survey localities were restricted further to those areas that we could access by road or ranch trails, or by travel with 4-wheel drive vehicles.

In Argentina, we focused our surveys on a random sample of sites within the previously defined main wintering range (with an emphasis on the less-developed coastal areas; see Buff-breasted Sandpiper habitat use in Blanco et al. 1993). We delineated survey plots by drawing a grid over the map of the main wintering range. Each plot was approximately 12 × 12 km in

size. Upon visiting each plot, observers selected a specific "locality" to survey based on habitat suitability. Thus only a small portion of each plot was actually surveyed during our study. We also conducted replicate surveys at one locality (Estancia Medaland) every 2 days (seven surveys) throughout the survey period (1–13 December 1999) to estimate population turnover. Buff-breasted Sandpipers were known to frequent this locality yearly and densities were moderate to high (Myers 1980, Isacch and Martínez 1999).

In Brazil, we also constructed a 12 × 12 km grid over the main wintering range and randomly selected a sample of these plots to survey. We followed the protocol of sampling a locality within each plot as described above for Argentina. Survey localities were in high terrain areas (approximately 8–20 m asl) above Pleistocene age fossil dune barriers and lower terrain areas (approximately 0–8 m asl) located in Holocenic lacustrine terraces of more recent origin (Long 1989). Localities were located predominantly in pastures, and active and abandoned rice fields.

In Uruguay, our sampling approach varied between years. During 1999, we surveyed road accessible portions of a narrow fringe of lowland surrounding three coastal lagoons (Castillos, Rocha, and Garzón) bordering the Atlantic Ocean. Due to logistic constraints these locations were not chosen randomly, but rather were placed in locations where Buff-breasted Sandpipers historically had been recorded in high numbers. In 2001, we expanded our survey areas to the entire main wintering range, and sampled random locations within a 12 × 12 km grid of plots as described above for Argentina. Survey localities were in pastures within or adjacent to fresh and saltwater marshes, and active and abandoned rice fields.

Survey methods.—We used variable circular plot sampling (Reynolds et al. 1980, Buckland et al. 1993) to survey Buff-breasted Sandpipers in each country. We chose this methodology because (1) Buff-breasted Sandpipers are very cryptic and are easier to detect by observers standing still, (2) patchily distributed habitats could be surveyed more easily, and (3) vegetation characteristics could be measured and identified with a particular survey location (Buckland et al. 1993). The total number of survey locations (points) per locality varied from 1–16 (most had ≥5 points), depending upon the amount of suitable habitat. At each point, 1–2 observers recorded the number, the behavior, and the radial distance from detected birds to the observation point (to the nearest meter). We recorded birds ≤250 m of each point, and points were spaced approximately 500 m apart to ensure observations were independent. We collected data for at ≥5 min at each point; observations lasted longer when observers could not record all birds near the point within 5 min, i.e., when large flocks were present. Although the time observers counted birds at each point varied, we do not feel this negatively biased our likelihood of detecting Buff-breasted Sandpipers at survey points with short observation periods. Indeed, Buff-breasted Sandpipers rarely flew into our observation area (i.e., ≤250 m of a point) after we had initiated counting; it simply took longer to count all the birds at survey points with large numbers of birds. We also recorded Buff-breasted Sandpipers between points and throughout the survey locality while walking to and from survey start and stop points. We used a handheld GPS receiver (Garmin GPS 12) to determine geographical coordinates for each survey point and Buff-breasted Sandpiper sighting (accurate to ≤50 m). Observers searched near the survey point first, and less intensively as the distance from the point increased. We placed emphasis on detecting Buff-breasted Sandpipers, followed by other shorebirds, and finally other bird species. Data were collected primarily during the morning and early afternoon (07:00–15:00), but occasionally in the evening.

Density estimate calculations.—We used the program DISTANCE (ver. 3.5, Thomas et al. 1998, http://www.ruwpa.st-and.ac.uk/distance/) to determine densities and confidence intervals for Buff-breasted Sandpipers detected in each country. We used clusters (or groups) of Buff-breasted Sandpipers as our sample unit. Data from each country (and each year for Uruguay) were analyzed separately to determine the most robust detection function, mean cluster size, and density estimate. This approach proved to be more robust than combining observations across countries due to the different detection functions in each country. For those countries where Buff-breasted Sandpipers were not detected near the survey point (possibly due to birds moving away from the point as observers approached), we left truncated the distance data to avoid calculating a biased low density estimate (Buckland et al. 1993). Similarly, we right truncated the distance data to remove outliers that contributed little to the density estimate and made modeling of the detection function difficult. A series of models then were tested and assessed for adequacy using Akaike's Information Criterion and the goodness of fit test. We also regressed group size against detection distance to test whether larger groups of Buff-breasted Sandpipers were more likely to be seen at greater distances from the survey point. This regression analysis was nonsignificant in all cases, allowing us to use the mean cluster size in our subsequent analyses.

RESULTS

Winter and migration range.—The first record of a Buff-breasted Sandpiper on the wintering grounds was in 1822 near Ipanema in São Paulo State in Brazil (Appendix 1, map location 72; Von Pelzeln 1870). Our search identified an additional 132 localities in South America where Buff-breasted Sandpipers had been detected at least once (Appendix 1, Figs. 1, 2). The largest number of localities was in Argentina (n = 48 or 36.1%), followed by Brazil with 30 (22.6%), and Uruguay and Peru with 11 (8.3%) each. Six other countries had

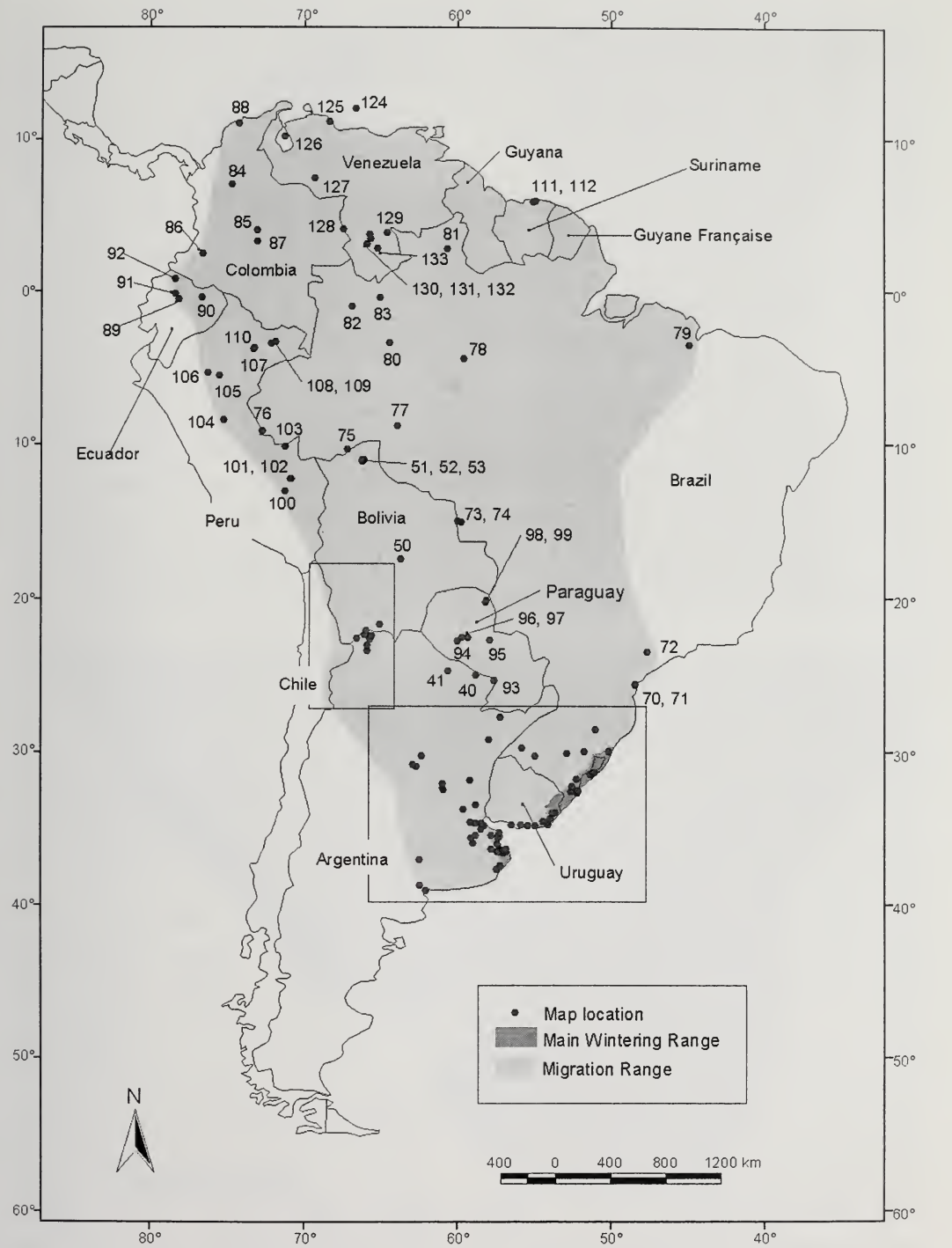

FIG. 1. Location of Buff-breasted Sandpiper sightings in South America, 1822–2000, and the main wintering and migration ranges. See Appendix 1 for attributes of the numbered locations. See Fig. 2 for the location and attribute numbers within the boxed areas.

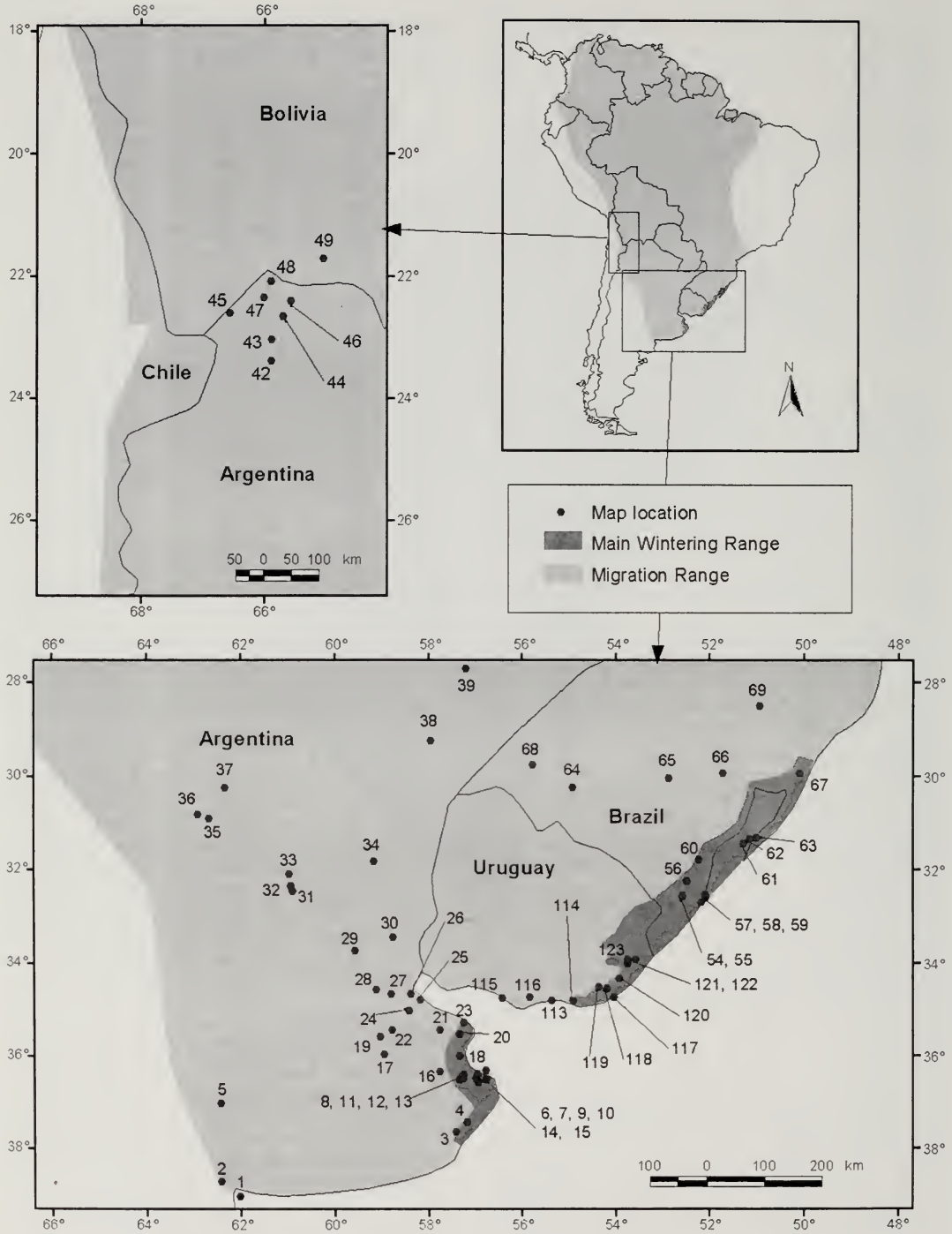

FIG. 2. Location of Buff-breasted Sandpiper sightings in the main wintering range of South America, 1822–2000. See Appendix 1 for attributes of numbered locations.

2–10 locations each (Appendix 1). Anecdotal reports indicate Buff-breasted Sandpipers are found in two of the three remaining countries of South America (Guyana and Guyane Française but not Chile), but information on exact locations was unavailable (Lanctot and Laredo 1994).

The year an observation occurred was recorded for 126 of the 133 localities (multiple observations were recorded at several localities). The largest percentage of observations occurred during 1992 and 1993 (n = 41, 24.4%), when surveys for Eskimo Curlews (*Numenius borealis*) were being conducted in Argentina and Uruguay (Blanco et al. 1993). Eighteen (10.7%) observations occurred prior to 1900, 21 (12.5%) between 1901 and 1938, 33 (19.6%) between 1943 and 1978, 32 (19.1%) between 1982 and 1991, and the remainder (n = 23, 13.7%) occurred between 1994 and 2000.

Seventy-five of the 133 localities included counts of the number of Buff-breasted Sandpipers (Appendix 1). Twenty-two localities included only subjective assessments of numbers such as present, common, and few. At 31 localities, the only information available was that a bird had been collected and a museum skin had been prepared. At the remaining five locations, the presence of museum skins and general information on the number of individuals present was recorded. The number of birds observed at each locality ranged from 1–2,000, but typically was <50. Thirteen groups of over 100 birds were documented, including 262 and 2,000 birds at Estancia Medaland (Argentina); 110 and 200 birds at Lagoa do Peixe (Brazil); "hundreds" at Estação Ecológica do Taim (Brazil); 500 birds at Hacienda La Corocora (Colombia); 140 birds at Bahía de Asunción (Paraguay); 143, 164, 216, and 225 birds at Laguna de Rocha and Arroyo La Palma (Uruguay); 210 at Bañado de las Maravillas (Uruguay); and 200 at Hato El Cedral (Venezuela; Appendix 1).

Historic information and more contemporary data indicate that the main wintering range of the species is within the coastal sectors of the Río de La Plata Grasslands (Soriano 1991), at the eastern portion of the flooding pampa of Argentina, and adjacent to large lagoon complexes in the coastal plain of Rio Grande do Sul of Brazil and Uruguay (Long 1989). The eastern portion of the flooding pampa is dedicated almost exclusively (>90%) to cattle ranching because flooding and salinity restrict agricultural development (León et al. 1984). Many recent records of Buff-breasted Sandpipers occurred in this area, primarily from San Miguel del Monte, General Lavalle region, Estancia Real Viejo, Estancia La Isolina, and Estancia Medaland (Appendix 1). The large concentrations of Buff-breasted Sandpipers from Uruguay and Brazil occurred in Laguna de Rocha and Bañados de las Maravillas in Uruguay; and from Estação Ecológica do Taim and Lagoa do Peixe in Brazil (Appendix 1).

Incidental sightings during winter also were reported in the remaining portions of the Río de La Plata Grassland (subregions of the rolling pampa, inland pampa, southern pampa, mesopotamic pampa). This area is characterized by extensive agriculture and human development. Smaller numbers also have been observed in saline lagoons of the Puna Ecoregion of Argentina and Bolivia, and the Central Trough of Rio Grande do Sul, Brazil.

The distribution of Buff-breasted Sandpiper sightings north of the wintering grounds indicates the species migrates through the Central Amazonia/Pantanal Flyway, crossing through the countries of Paraguay, Bolivia, Brazil, Peru, Colombia, Venezuela, and Suriname on their way north to the Central Flyway of North America (Fig. 1; see also Antas 1983). Migration south appears to occur along a similar route. Buff-breasted Sandpipers frequently were reported using sand bars along rivers in the interior portions of South America; most records are from the Amazonian sectors of Bolivia, Brazil, Colombia, Ecuador, Peru and Venezuela. The number of birds detected typically was small, although in a few cases the species was listed only as "present."

Contemporary distribution and abundance.—Results of the circular plot sampling are presented in Table 1. In Argentina, 5–7 people surveyed 32 localities (296 survey points) from 1–13 December, 1999. Buff-breasted Sandpipers were present on 10 of the 32 localities surveyed in Argentina (Fig. 3). We found the species in two distinct areas: southern Bahía Samborombón (General Lavalle District, localities 9, 12–17, and 19; Fig. 3) and north of Mar Chiquita coastal lagoon

TABLE 1. Buff-breasted Sandpiper sightings during variable circular plot sampling in Argentina, Uruguay, and Brazil. See Figures 3–5 for location of map numbers.

Map number	Locality[a]	Latitude (S)	Longitude (W)
Argentina, 1999			
1	Vergara	35° 23′ 59″	57° 39′ 23″
2	Don Cipriano	35° 28′ 54″	57° 47′ 20″
3	W of Don Cipriano	35° 31′ 14″	57° 37′ 13″
4	Pipinas	35° 32′ 45″	57° 20′ 21″
5	Giribone	35° 37′ 24″	57° 38′ 36″
6	W of Libres del Sud	35° 39′ 00″	57° 38′ 25″
7	SE of Libres del Sud	35° 46′ 15″	57° 40′ 47″
8	Canal de las Escobas	35° 59′ 42″	57° 38′ 04″
9	Canal A (Ea. Santa Lucia)	36° 12′ 24″	57° 18′ 15″
10	Laguna del Junco	36° 15′ 41″	57° 34′ 01″
11	S of Santa Magdalena	36° 21′ 15″	57° 27′ 59″
12	Canal Sta. Clara	36° 24′ 07″	57° 15′ 02″
13	Reserva Campos del Tuyu	36° 24′ 32″	56° 50′ 43″
14	Ea. La Victoria	36° 24′ 55″	57° 18′ 47″
15	W of Ea. El Recuerdo	36° 26′ 12″	57° 23′ 13″
16	SW of General Conesa	36° 30′ 08″	57° 14′ 33″
17	Ea. La Isolina	36° 32′ 49″	56° 55′ 50″
18	S of Ea. Santa Catalina	36° 33′ 39″	57° 22′ 46″
19	E of Ea. El Tonetera	36° 33′ 55″	57° 05′ 28″
20	Close to Ea. Cari Lauquen	36° 38′ 52″	57° 11′ 36″
21	Ea. La Emestina	36° 40′ 31″	56° 51′ 40″
22	Route 56 surroundings	36° 45′ 09″	57° 16′ 33″
23	Ea. Las Trea Marías	36° 53′ 05″	57° 10′ 55″
24	Ea. San Jose	36° 55′ 53″	56° 49′ 40″
25	Colonia Tío Domingo	37° 02′ 08″	56° 57′ 43″
26	Ea. La Susana	37° 16′ 39″	57° 41′ 04″
27	N of Ea. Medaland	37° 24′ 22″	57° 09′ 58″
28	N of Nanuel Rucá	37° 31′ 37″	57° 36′ 49″
29	Ea. Mar Chiquita	37° 41′ 30″	57° 23′ 33″
30	W of El Dorado	37° 44′ 30″	57° 47′ 46″
31	El Cangrejal	37° 46′ 30″	57° 31′ 14″
32	Ea. Medaland[e]	37° 25′ 55″	57° 11′ 49″
Brazil, 2001			
1	Varzinha	30° 18′ 32″	50° 52′ 07″
2	Ponta do Anastácio	30° 27′ 47″	50° 40′ 50″
3	Bacopari	30° 33′ 04″	50° 26′ 43″
4	Lagoa da Figueira	30° 48′ 48″	50° 39′ 58″
5	Cristóvão Pereira	31° 05′ 56″	51° 01′ 44″
6	Lagoa do Peixe Nat. Park	31° 15′ 27″	50° 59′ 22″
7	S and within Lagoa do Peixe Nat. Park	31° 26′ 46″	51° 10′ 03″
8	Capão da Areia marsh	31° 33′ 21″	51° 17′ 22″
9	Ilha da Torotama	31° 55′ 35″	52° 10′ 58″
10	Saco da Mangueira	32° 06′ 52″	52° 08′ 09″
11	Granja 4 Irmãos	32° 17′ 47″	52° 31′ 46″
12	N of Banhado do Taim	32° 31′ 59″	52° 32′ 20″
13	arroio del Rei	32° 57′ 40″	53° 04′ 48″
14	Vargem Grande	33° 10′ 14″	53° 12′ 07″
15	Curral do Arroio	33° 17′ 18″	53° 25′ 15″
16	arroio do Pastoreio	33° 18′ 16″	53° 03′ 28″
17	W of Santa Vitória do Palmar	33° 27′ 40″	53° 25′ 43″
18	E of Santa Vitória do Palmar	33° 35′ 07″	53° 18′ 52″

TABLE 1. EXTENDED

Map number	Date	Survey points	Number on points[b]	Number between points[c]	Number at nearby sites[d]	Total
Argentina, 1999						
1	13 Dec 99	5	0	0	0	0
2	11 Dec 99	10	0	0	0	0
3	11 Dec 99	6	0	0	0	0
4	11 Dec 99	5	0	0	0	0
5	10 Dec 99	5	0	0	0	0
6	10 Dec 99	5	0	0	0	0
7	10 Dec 99	5	0	0	0	0
8	9 Dec 99	10	0	0	0	0
9	12 Dec 99	6	5	2	23	30
10	10 Dec 99	10	0	0	0	0
11	7 Dec 99	10	0	0	0	0
12	6 Dec 99	11	23	40	0	63
13	4 Dec 99	11	62	20	0	82
14	7 Dec 99	10	3	0	6	9
15	6 Dec 99	10	5	1	0	6
16	5 Dec 99	10	0	10	0	10
17	1 Dec 99	16	10	1	4	15
18	5 Dec 99	10	0	0	0	0
19	3 Dec 99	7	0	2	9	11
20	3 Dec 99	4	0	0	0	0
21	8 Dec 99	10	0	0	0	0
22	3 Dec 99	11	0	0	0	0
23	8 Dec 99	10	0	0	0	0
24	7 Dec 99	16	0	0	0	0
25	5 Dec 99	11	0	0	0	0
26	3 Dec 99	10	0	0	0	0
27	9 Dec 99	10	45	2	5	52
28	2 Dec 99	10	0	0	0	0
29	6 Dec 99	10	0	0	0	0
30	4 Dec 99	11	0	0	0	0
31	8 Dec 99	10	0	0	0	0
32	1 to 13 Dec 99	11	29.4	5.7	46.6	81.7
	Total	296	182	84	94	360
Brazil, 2001						
1	2 Dec 01	10	0	0	0	0
2	14 Dec 01	9	17	12	0	29
3	13 Dec 01	5	0	0	0	0
4	11 Dec 01	10	0	0	0	0
5	13 Dec 01	6	16	190	0	206
6	12 Dec 01	9	146	3	0	149
7	12 Dec 01	10	309	124	11	444
8	13 Dec 01	10	108	79	0	187
9	4 Dec 01	10	457	157	186	800[f]
10	3 Dec 01	10	4	0	0	4
11	5 Dec 01	10	0	0	0	0
12	6 Dec 01	12	97	25	16	138
13	7 Dec 01	10	0	0	0	0
14	8 Dec 01	10	0	0	0	0
15	8 Dec 01	10	0	0	0	0
16	7 Dec 01	10	5	31	0	36
17	9 Dec 01	10	72	16	0	88[f]
18	9 Dec 01	10	0	0	0	0
	Total	171	1231	637	213	2081

TABLE 1. CONTINUED

Map number	Locality[a]	Latitude (S)	Longitude (W)
Uruguay, 1999			
1	N of Laguna de Castillos	34° 13′ 13″	53° 55′ 10″
2	NE of Laguna de Castillos	34° 15′ 08″	53° 53′ 26″
3	E of Laguna de Castillos	34° 19′ 08″	53° 51′ 44″
4	SE of Laguna de Castillos	34° 19′ 50″	53° 51′ 11″
5	NE of Laguna de Rocha	34° 31′ 49″	54° 15′ 17″
6	N of Laguna de Rocha	34° 33′ 05″	54° 18′ 24″
7	N of Laguna de Rocha	34° 34′ 02″	54° 18′ 49″
8	E of Laguna de Rocha	34° 34′ 50″	54° 14′ 04″
9	NW of Laguna de Rocha	34° 37′ 18″	54° 24′ 38″
10	SE of Laguna de Rocha	34° 40′ 50″	54° 16′ 17″
11	W of Laguna de Rocha	34° 41′ 40″	54° 19′ 31″
12	W of Laguna de Rocha	34° 42′ 29″	54° 23′ 16″
13	S of Laguna Garzón	34° 47′ 34″	54° 33′ 25″
Uruguay, 2001			
1	Pta. Cachimbas	32° 42′ 24″	53° 17′ 45″
2	Pta. Catumbera	32° 50′ 18″	53° 19′ 36″
3	Zapata stream	32° 55′ 44″	53° 35′ 58″
4	Cebollatí surroundings	33° 14′ 01″	53° 42′ 26″
5	Picada de Techera	33° 20′ 32″	54° 07′ 45″
6	N of Laguna Negra	33° 54′ 18″	53° 44′ 00″
7	Castillos surroundings	34° 12′ 29″	53° 53′ 19″
8	E of Laguna de Castillos	34° 20′ 17″	53° 50′ 49″
9	W of Laguna de Castillos	34° 20′ 55″	53° 59′ 39″
10	NW of Laguna de Rocha	34° 35′ 35″	54° 19′ 30″
11	E of Laguna de Rocha	34° 39′ 04″	54° 15′ 03″
12	Ea. La Rinconada	34° 39′ 39″	54° 20′ 02″
13	E of Laguna Garzón	34° 45′ 34″	54° 31′ 42″
14	E of Laguna José Ignacio	34° 48′ 03″	54° 41′ 04″

[a] "Ea." refers to an estancia or ranch. Directions from a locality are capitalized single or double letters (e.g., E, NW). Otherwise localities refer to nearby towns, cities, or distinct geographic landmarks.
[b] Number of Buff-breasted Sandpipers detected within 250 meters of survey points.
[c] Number of Buff-breasted Sandpipers detected while walking between survey points.
[d] Number of Buff-breasted Sandpipers detected while walking to and from plot.
[e] Values for Ea. Medaland represent mean values over 7 surveys.
[f] Numbers represent minimum values as birds were flying around and could not be reliably counted between points.
[g] Mean values for Uraguay are used in this summary.

(localities 27 and 32; Fig. 3). We counted 360 Buff-breasted Sandpipers at these 10 localities. We detected most (182) birds on point surveys, with fewer individuals detected between points and between survey localities. Only once did we detect the majority of Buff-breasted Sandpipers after we completed a survey (locality 9). The total number of Buff-breasted Sandpipers detected at each locality varied from 0–82. The mean number of birds detected per point at each locality varied from 0–5.64, with the highest numbers at Reserve Campos del Tuyú, Estancia Medaland and Canal Sta. Clara. We calculated that 0.11 Buff-breasted Sandpipers/ha were present on the 31 localities in Argentina (excluding Estancia Medaland which was surveyed repeatedly; Table 2).

In Brazil, 5–9 people surveyed 18 localities (171 survey points) from 2–13 December 2001. Buff-breasted Sandpipers were present on 10 of the 18 localities surveyed in Brazil (Fig. 4). We found the species primarily along the southern and western edge of Lagoa do

TABLE 1. CONTINUED, EXTENDED

Map number	Date	Survey points	Number on points[b]	Number between points[c]	Number at nearby sites[d]	Total
Uruguay, 1999						
1	19 Dec 99	5	0	0	0	0
2	19 Dec 99	5	44	18	6	68
3	19 Dec 99	5	8	14	48	70
4	19 Dec 99	5	58	20	0	78
5	17 Dec 99	5	48	19	0	67
6	16 Dec 99	5	110	77	0	187
7	18 Dec 99	3	3	19	17	39
8	18 Dec 99	6	0	7	0	7
9	18 Dec 99	8	1	2	0	3
10	17 Dec 99	1	1	0	0	1
11	17 Dec 99	4	69	0	0	69
12	17 Dec 99	3	33	0	0	33
13	16 Dec 99	4	59	5	0	64
	Total	59	434	181	71	686
Uruguay, 2001						
1	6 Dec 01	10	0	0	0	0
2	7 Dec 01	9	25	0	0	25
3	7 Dec 01	10	0	0	0	0
4	8 Dec 01	5	0	0	0	0
5	5 Dec 01	10	0	0	0	0
6	9 Dec 01	9	19	82	0	101
7	4 Dec 01	10	0	0	0	0
8	12 Dec 01	10	84	40	0	124
9	12 Dec 01	10	212	139	0	351
10	3 Dec 01	10	106	91	0	197
11	10 Dec 01	10	26	59	0	85
12	10 Dec 01	10	73	249	178	500
13	11 Dec 01	5	3	1	0	4
14	11 Dec 01	10	4	2	0	6
	Total	128	552	663	178	1393
	Total for all countries[g]	561	1906	1143	431	3480

Peixe (localities 5–8; Fig. 4), Ilha da Torotama (locality 9; Fig. 4), north of Banhado do Taim (locality 12; Fig. 4), and west of Santa Vitória do Palmar (locality 17; Fig. 4). We counted 2,081 Buff-breasted Sandpipers at these 10 localities. We detected 60% (n = 1,231) of the birds on point surveys, with the remainder detected between points and between survey localities. Twice we detected the majority of Buff-breasted Sandpipers after we completed a survey (localities 5 and 16). The total number of Buff-breasted Sandpipers detected at each locality varied from 0–800. The mean number of birds detected per point at each locality varied from 0–45.7, with the highest numbers at Ilha da Torotama and near Lagoa do Peixe National Park. We calculated that 1.62 Buff-breasted Sandpipers/ha were present on the 18 localities in Brazil (Table 2).

During the 1999 surveys in Uruguay, 2–4 people surveyed 13 localities (59 survey points) from 16–19 December 1999. Buff-breasted Sandpipers were present on 12 of 13 localities surveyed in Uruguay (Fig. 5). We found birds all around Laguna de Rocha (localities 5–12; Fig. 5), the northeast and east sides of Laguna de Castillos (localities 2–4; Fig. 5), and the south side of Laguna Garzón (locality 13; Fig. 5); we detected a total of 686 Buff-breasted Sandpipers at these 12 localities. The majority (434) was detected during point surveys, except at two localities where the majority was detected after the survey was completed (localities 3 and 7). The total num-

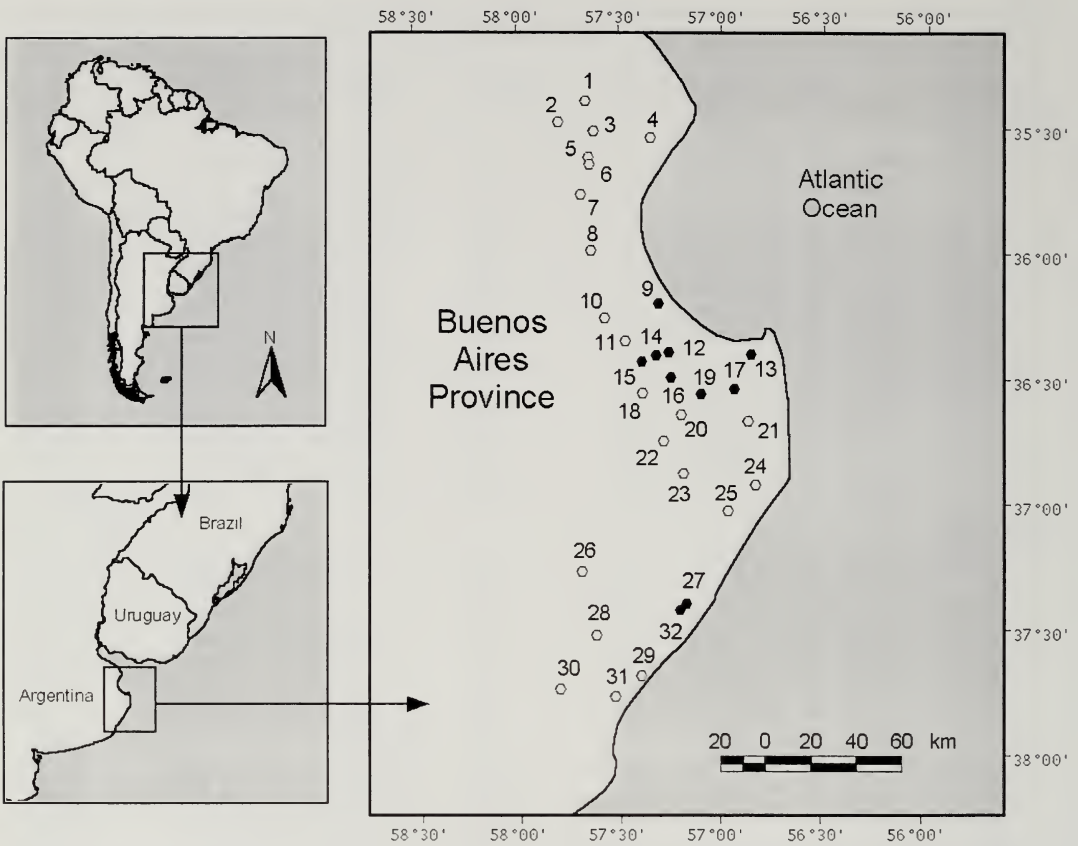

FIG. 3. Locations surveyed and presence (dark circles) of Buff-breasted Sandpipers on survey localities in Argentina during December 1999. See Table 1 for attributes of each locality.

ber of Buff-breasted Sandpipers detected at each locality varied from 0–187, with the highest numbers on the north and west sides of Laguna de Rocha, eastern edge of Laguna de Castillos, and south of Laguna Garzón. The density of Buff-breasted Sandpipers in Uruguay was higher than in Argentina and Brazil; 2.18 Buff-breasted Sandpipers/ha were present on the 13 localities in Uruguay (Table 2).

During 2001, we conducted surveys over a larger geographic area and in a random fashion throughout the main wintering area of

TABLE 2. Number of plots, survey points, and counts of Buff-breasted Sandpipers used in calculations of density for each country using the program DISTANCE.[a]

Country	Number of plots	Number of survey points	Number of clusters (number of individuals)	Mean ± SE cluster size	Detection range (m)[b]	Density (individuals/ha)	Density 95% C.I.
Argentina, 1999	31	285	62 (141)	2.27 ± 0.22	0 to 150	0.11	0.04–0.31
Brazil, 2001	18	171	344 (1202)	3.49 ± 0.40	25 to 220	1.62	0.67–3.93
Uruguay, 1999[c]	13	59	75 (405)	5.40 ± 0.75	20 to 210	2.18	0.89–5.31
Uruguay, 2001[c]	14	128	89 (531)	5.96 ± 1.26	10 to 235	1.08	0.37–3.18

[a] Number of points and individuals used in these analyses was lower than that reported in Table 1 because data were limited to birds observed within the detection range of each country.

[b] Determined by plotting the detection distance of all observations and then eliminating outliers that would make modeling the detection probability difficult (see Buckland et al. 1993).

[c] The different methods of selecting survey localities between years (see text) probably resulted in artificially high density estimates in 1999.

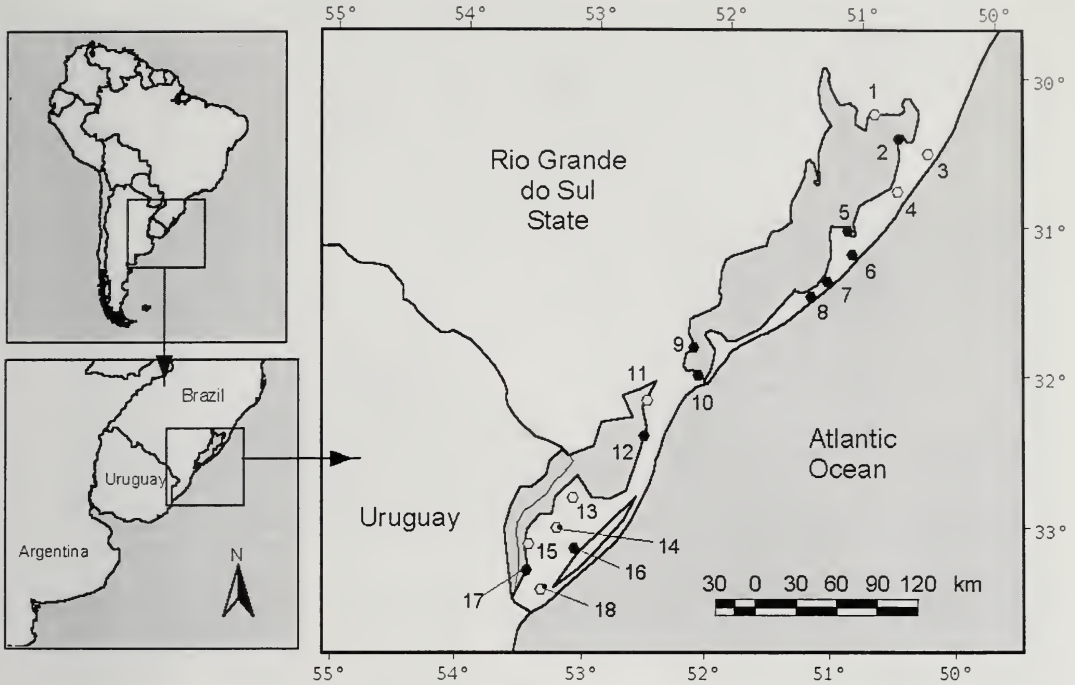

FIG. 4. Locations surveyed and presence (dark circles) of Buff-breasted Sandpipers on survey localities in Brazil during December 2001. See Table 1 for attributes of each locality.

Uruguay. Although the number of localities surveyed (14) was similar to that of 1999 (13), the number of survey points increased from 59 to 128. We conducted surveys approximately one week earlier during 2001 (3–12 December during 2001 compared to 16–19 December during 1999). Buff-breasted Sandpipers were present on 9 of 14 localities surveyed (Fig. 5). As during 1999, we found birds around Laguna de Rocha (localities 10–12; Fig. 5), Laguna de Castillos (localities 8 and 9; Fig. 5), and the south side of Laguna Garzón (locality 13; Fig. 5). These observations mirrored the historic distribution of the species (Fig. 2). We detected 1393 Buff-breasted Sandpipers at these nine localities. We detected 40% (552) during point surveys. The total number of Buff-breasted Sandpipers detected at each locality varied from 0–500, with the highest numbers on the north and west sides of Laguna de Rocha, and western and eastern edges of Laguna de Castillos. Our density estimate for Uruguay was lower in 2001 (1.08 individuals/ha; Table 2) than in 1999.

Turnover rates.—The number of Buff-breasted Sandpipers detected during seven surveys at Estancia Medaland varied from 9–302 birds (mean = 81.7 ± 99.1 SD, n = 7; Fig. 6) over a 13-day period in December 1999. Most of this variation was due to a flock of 266 Buff-breasted Sandpipers detected after the survey was completed on 13 December. When we limited the data to birds counted at survey points, the number of individuals ranged from 9–60 per survey, with a median of 33 and a mean of 29.4 (SD = 17.0, n = 7). The number of birds counted at survey points followed a binomial distribution, with an initial peak on the second and third surveys, and a second higher count on the sixth survey. The probability of detecting birds at a given point varied greatly. Three of the 11 survey points did not have Buff-breasted Sandpipers present on any survey day, whereas one point had birds present on 5 days. The mean number of Buff-breasted Sandpipers detected at each point varied from 0.0–14.1 across the seven surveys.

Habitat associations.—To determine habitat use by Buff-breasted Sandpipers we first excluded plots that were selected nonrandomly

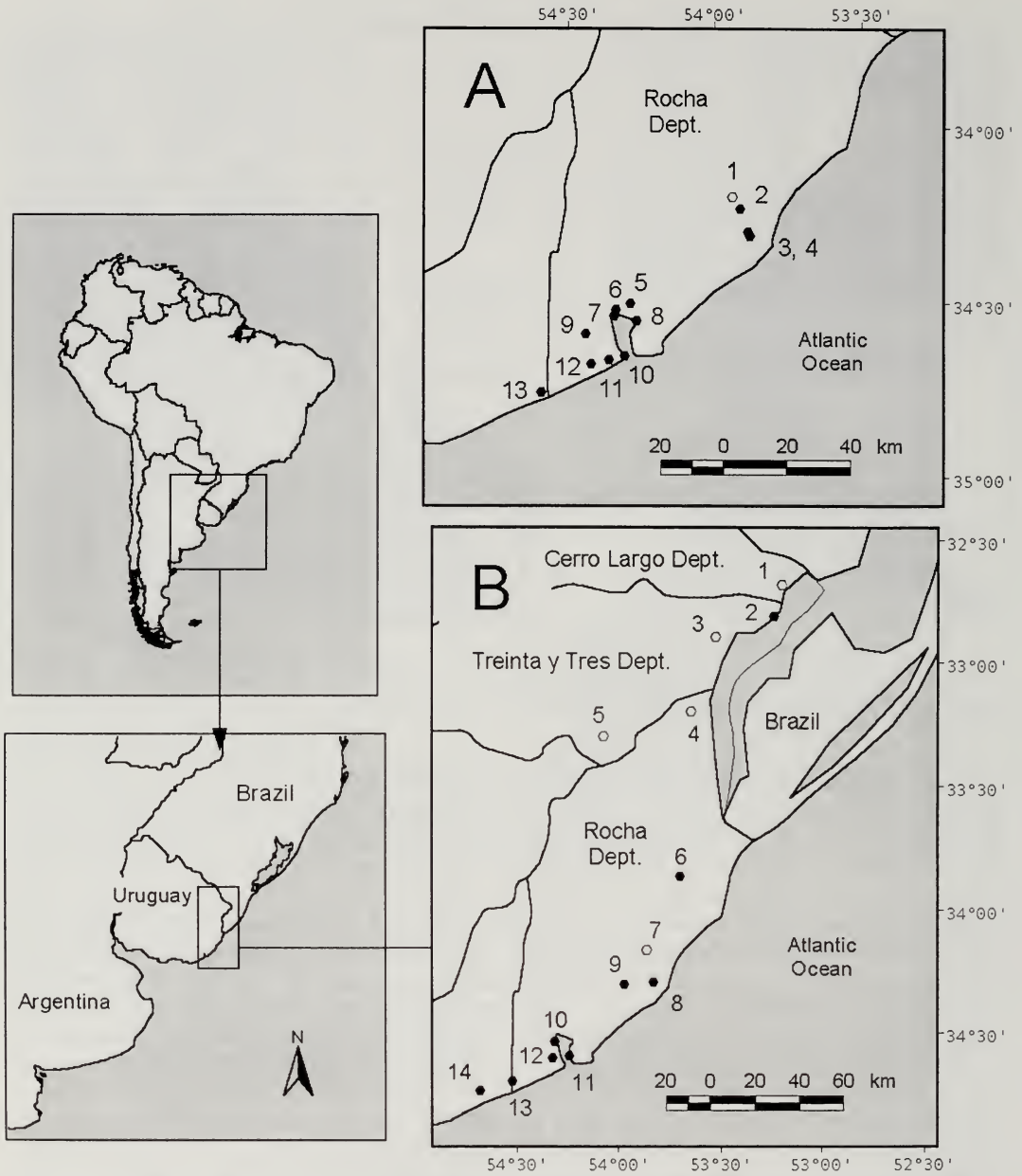

FIG. 5. Locations surveyed and presence (dark circles) of Buff-breasted Sandpipers on survey localities in Uruguay during (A) December, 1999, and (B) December, 2001. See Table 1 for attributes of each locality.

(plots from the 1999 survey in Uruguay) or repeatedly surveyed within a year (Estancia Medaland in Argentina). After excluding these areas, we detected Buff-breasted Sandpipers at 122 survey points (20.9% of 584 points) distributed in 28 localities (44.4% of 63 localities). We detected most Buff-breasted Sandpipers at survey points located in pasturelands (85.8%), whereas a smaller percentage were found in agriculture (6.7%) and abandoned fields (7.5%). The survey points where we detected Buff-breasted Sandpipers usually were grazed by livestock (90%), had relatively short vegetation (the dominant veg-

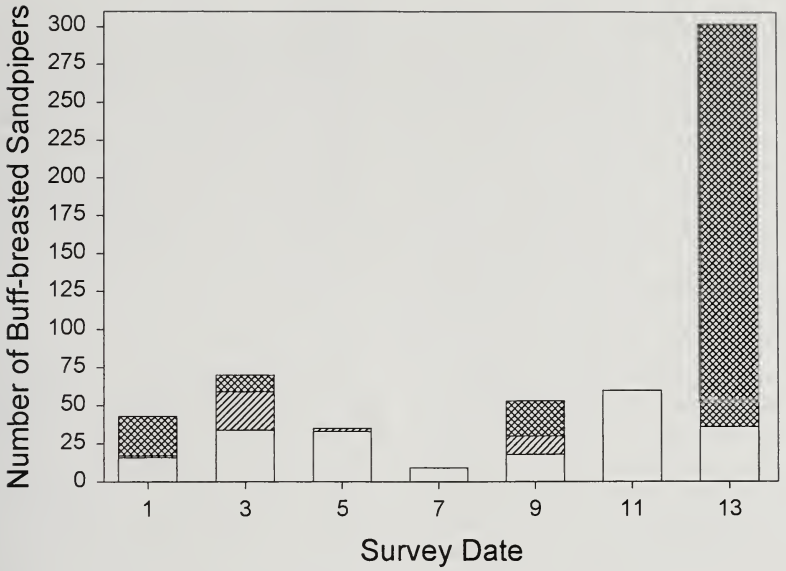

FIG. 6. Number of Buff-breasted Sandpipers detected at Estancia Medaland, Argentina, 1–13 December 1999. White areas represent birds counted at survey points, diagonal line areas represent birds counted between points, and checkered areas represent birds counted between survey locations.

etation for 90% of the points was <10 cm tall), and frequently were grazed intensively (the dominant cover type for 62% of points was vegetation 2–5 cm tall, representing >49% of ground cover).

In Brazil and Uruguay, we found Buff-breasted Sandpipers almost exclusively in heavily grazed grasslands along the margins of salt and freshwater lagoons on relatively recent terrain of Quaternary age. Although we sampled areas of seemingly suitable habitat on geologically older terrain, Buff-breasted Sandpipers were associated consistently with Holocenic coastal plains below the barrier of old dunes. These dunes were shaped during the last major marine transgression in southern Brazil and eastern Uruguay approximately 5,000–7,000 ybp. We occasionally found Buff-breasted Sandpipers in agricultural or abandoned fields (17.4% of all survey points that occurred in these countries).

In Argentina, we found Buff-breasted Sandpipers exclusively in pasturelands. Unlike Brazil and Uruguay, these pastures were part of large ranches and were not restricted to lagoon margins. Indeed, the amount of apparently suitable habitat in Argentina was much larger relative to Brazil and Uruguay, as pasturelands covered a large portion of the pampas. The geographic extent of the grasslands coincides with the old albufer region that borders Bahía Samborombón; this old albufer region appears to explain the main wintering distribution of the species in Argentina.

DISCUSSION

Contemporary abundance of Buff-breasted Sandpipers.—Brazil, followed by Uruguay (on average), and Argentina had the highest population densities of Buff-breasted Sandpipers. Density estimates ranged from 0.11 birds/ha in Argentina to 2.18 in Uruguay, both based on surveys from 1999. Because we conducted our surveys in habitats most likely to contain Buff-breasted Sandpipers, these density estimates probably represent the maximum densities for any area in their respective country. Unfortunately, a comparison among the four sample locations (country and year combinations) is hampered by several confounding factors. First, the location and number of plots varied between survey years in Uruguay. The higher density estimates for 1999 probably resulted from the nonrandom selection of survey sites that year. After comparing our data between years, it appears that our surveys during 1999 were conducted in areas with some of the higher densities of

Buff-breasted Sandpipers. Second, surveys were not conducted during the same year in all three countries. Accordingly, environmental differences among countries and years may have confounded our comparisons. For example, Argentina had record levels of rainfall during 2001, resulting in grasslands being flooded and unavailable to Buff-breasted Sandpipers (RBL and DEB unpubl. data). This flooding appeared to have reduced the number of Buff-breasted Sandpipers based on counts of birds at a few localities visited during both 1999 and 2001 (RBL and DEB unpubl. data). The decrease in habitat availability may have caused Buff-breasted Sandpipers to use other less appropriate areas in Argentina or return to Brazil and Uruguay in search of suitable winter habitat. This scenario would result in higher than normal densities in Brazil and Uruguay relative to other years. However, a comparison of a few sites in Uruguay and Brazil visited during both years of our study does not confirm this; some sites had more birds during 2001 and others had fewer (Table 1). It also is possible that our density estimates for each country are accurate, and that the higher densities in Brazil and Uruguay simply reflect suitable land area. Wintering range sizes depicted in Figure 2 and our knowledge of the countries indicate suitable land is more abundant in Argentina, possibly allowing birds to distribute more evenly and in lower densities across the landscape.

Flock movement within and between years.—The moderately large confidence intervals around our population density estimates reflect the large variation in Buff-breasted Sandpiper numbers detected at the surveyed localities. This variation is especially apparent for Estancia Medaland (Fig. 6). Buff-breasted Sandpiper numbers varied from 9–302 birds during the seven surveys conducted at the estancia. The large influx of Buff-breasted Sandpipers (266 birds) on 13 December suggests this species aggregates in large flocks that move frequently. We also observed large flocks in Uruguay and Brazil at a few localities, and large flocks were present in the historic data (Appendix 1). In addition, we regularly observed flocks away from survey points. If birds were missed during surveys for either of these reasons, the population density would be underestimated. The DISTANCE program partially compensates for this problem by correcting for cluster size and the probability of detecting birds. Nevertheless, additional study is needed to determine how the species aggregates throughout the austral summer, the timing and level of movement by Buff-breasted Sandpipers across their wintering range, and the scale at which surveys must be conducted to ensure accurate population estimates can be made.

Changes in historic distribution and abundance of Buff-breasted Sandpipers.—Our surveys found Buff-breasted Sandpipers throughout most of their historic wintering range. The species was conspicuously absent, however, from areas just south of the city of Buenos Aires. This region has undergone extensive urban development and contains little suitable habitat today. Interior portions of the pampas also have become less desirable for Buff-breasted Sandpipers as ranch lands have been converted to agriculture (Oesterheld 1993). We found no evidence to support Wetmore's (1927) suggestion that a southern wintering range near the mouths of Colorado and Negro rivers in northern Patagonia exists. Our surveys did allow us to record more accurately the distribution of birds within the historic wintering range. For example, we observed Buff-breasted Sandpipers along the border between Brazil and Uruguay (localities 16 and 17, Fig. 4; locality 2, Fig. 5B). Belton (1994) indicated Buff-breasted Sandpipers were in this area but provided no definitive locations.

The number of Buff-breasted Sandpipers detected during our surveys appeared to be far below historic levels. Indeed, W. H. Hudson, in Buenos Aires Province in 1868, reported ". . . flocks of about one to two or three hundred, flying low and very swiftly due north, flock succeeding flock at intervals of about 10 or 12 min; and this migration continued for [at least] three days . . . " (Hudson 1920). This single observation greatly surpasses the 360 birds detected by our team during 13 days of surveys in Argentina. Information from the migration routes and breeding grounds also suggests Buff-breasted Sandpipers have declined. Singley (1893), McIlhenny (1943), and Forbush (1912) listed the species as very common in the meat markets of Texas, Louisiana, and Massachusetts during the mid to late 1800s. The species also was described as an

"abundant summer resident" on its breeding grounds at Point Barrow, Alaska, during 1880 (Murdoch 1885). Recent reports from all these locations indicate the species occurs rarely and/or sporadically (McIlhenny 1943, Forbush 1978, Johnson and Herter 1989, Lanctot and Weatherhead 1997). Unfortunately, systematic surveys were not conducted on the wintering grounds during the late 1800s, making comparisons to our survey density estimates impossible.

Contemporary changes in Buff-breasted Sandpiper abundance.—Several lines of evidence suggest the population of Buff-breasted Sandpipers is continuing to decline. A comparison of population numbers on the wintering grounds at Estancia Medaland, Argentina, between 1973 and the 1990s suggests the species has decreased greatly. Myers (1980) estimated that ≤2,000 Buff-breasted Sandpipers used this area during the austral summers of 1973 and 1974, whereas population surveys between 1996 and 2000 indicated that no more than 200 birds used this area (Isacch and Martínez 1999; JPI and M. Martínez unpubl. data).

Information from the breeding grounds also suggests a decline in population size. A comparison of Buff-breasted Sandpiper densities at 38 plots near Creswell Bay, Somerset Island (Nunavut, Canada), showed a significant decrease in densities from 1995 and 1997 to 2001 (P. Latour and J. Bart unpubl. data). Information from two migration sites also confirms this decline. L. Morris (pers. comm.) observed thousands of Buff-breasted Sandpipers near Benedict, Nebraska, during the mid-1980s, but now observes <100 each year. D. Dekker (pers. comm.) reports a similar decline from the 1970s to early 1990s near Beaverhill Lake, Edmonton, Alberta. Unfortunately, insufficient data are available from the broader Maritimes Shorebird Survey (covering sites in eastern Canada) and the International Shorebird Survey (covering sites in the eastern and central U.S.) to test for an increase or decrease in Buff-breasted Sandpiper numbers (J. Bart unpubl. data). Although it is possible that the decline in bird numbers described above are a result of birds shifting their winter, migration, and breeding distributions, these data suggest caution should be used when managing the species until additional trend data can be gathered.

South American migration.—The distribution of Buff-breasted Sandpiper sightings suggests that the species migrates through the central portions of South America on its way to and from the wintering range in Argentina, Uruguay, and Brazil (see also Antas 1983). The paucity of Buff-breasted Sandpiper sightings in the interior regions of South America may be due, in part, to a lack of observers (but see Hayes et al. 1990, Stotz et al. 1992). Suitable habitat probably is limited, however, as shorebirds appear to be restricted to river floodplains exposed during the dry seasons and cattle ponds and casual water in newly cleared areas of forest (Hayes and Fox 1991, Stotz et al. 1992). These variable habitat conditions might require Buff-breasted Sandpipers to make a direct flight over the Amazonia regions in some years (Terborgh 1989), especially during the northward migration when water levels tend to be high. It seems unlikely that Buff-breasted Sandpipers use the eastern and western coasts of South America during migration as ornithologists have studied these areas thoroughly and found few (e.g., Wilson et al. 1998, Rodrigues 2000). It is possible that some individuals migrate along the coasts making few landings.

Important sites and their protection/management.—We identified several important areas in each country for wintering Buff-breasted Sandpipers. In Argentina, we verified the continued importance of Estancia Medaland as a major wintering site (Myers 1980), and discovered the pasturelands in southern Bahía Samborombón. Vast ranches within the latter area accounted for 63% of the total number of Buff-breasted Sandpipers detected in Argentina. In Uruguay and Brazil, our surveys indicated intensively grazed pasturelands near several of the lagoon systems had large numbers of Buff-breasted Sandpipers. Indeed, some of the largest groups of Buff-breasted Sandpipers ever recorded were detected at Ilha da Torotama and Lagoa do Peixe National Park in Brazil, and Laguna de Rocha and Laguna de Castillos in Uruguay.

Most of the sites identified as being key wintering areas in this study are privately owned and few are legally protected, although these areas are unlikely to be converted to ag-

riculture because of flooding and saline conditions near the coast. However, these areas are likely to be flooded should global warming lead to higher water levels. Land management practices in unprotected areas farther inland are subject to change with global and regional economic constraints. Indeed, Oesterheld (1993) reported large fluctuations in the proportion of land devoted to cropping and ranching in the Río de la Plata Grassland during the past 20–30 years. These changes appear to be directly related to the price of grain and beef.

Other forms of development, such as mines and pine plantations in Brazil, construction of roads and buildings for tourism in Brazil and Uruguay, and the subdivision of ranches in Argentina, also may have a negative effect on the species (Sagrera 1999; G. Maurício pers. comm., GAB and JPI unpubl. data). So far, pine plantations are restricted mostly to upland areas within Brazil, and seedlings have been unable to become established in suitable Buff-breasted Sandpiper habitat because of livestock grazing. During the past year, biologists were able to negotiate the location of an approximately 8,000-ha mine project south of Lagoa do Peixe, Brazil, to habitats not used by Buff-breasted Sandpipers. Further, this mine site is to be approved under the condition that the Capão da Areia marsh be protected and added to the Lagoa do Peixe National Park (GAB unpubl. data). Both areas currently are used extensively by Buff-breasted Sandpipers. Control of tourism in Uruguay appears less certain, and the effect of subdividing estancias on Buff-breasted Sandpiper habitat in Argentina is unknown.

The value of livestock pastures to Buff-breasted Sandpipers is dependent upon appropriate ranch management. The introduction and movement of livestock at a local and regional level may indirectly have strong within- and among-year effects on the distribution and abundance of Buff-breasted Sandpipers. For example, pastures where grazing has only recently begun may not be suitable for Buff-breasted Sandpipers, but in a few weeks these same pastures might be of the correct vegetation height. Observations at a limited number of sites visited during both years of our study confirmed this. Areas with intensive grazing in 1999 had Buff-breasted Sandpipers present but these same areas had no birds when grass heights were higher in 2001 (and vice versa). Additionally, pastures may never become suitable if livestock are moved too frequently among pastures (to minimize overgrazing), introduced too late in the austral summer, or removed altogether. The latter scenario may be particularly common when land is acquired by conservation agencies and the livestock are removed to benefit other wildlife species. While advocating protection of areas for all wildlife, we believe a portion of these areas should be managed to maintain pasturelands. Ideally, these areas should be managed so that parcels of land with short vegetation are available throughout the austral summer to accommodate early-, mid-, and late-wintering Buff-breasted Sandpipers. Such a grassland management plan will benefit other Nearctic (e.g., American Golden-Plovers, *Pluvialis dominica*) and Patagonian migratory shorebirds (e.g., Rufous-chested Dotterel, *Charadrius modestus*; Tawny-throated Dotterel, *Oreopholus ruficollis*) that also use these areas (JPI and M. Martínez unpubl. data).

In Brazil and Uruguay, Buff-breasted Sandpipers also are vulnerable to the loss of suitable habitat that is quite limited and restricted geographically. Our observations suggest Buff-breasted Sandpipers use a very limited area, stretching over a very narrow zone of recent terrain at ocean shores and around some coastal lagoons. While generally grazed by livestock, the natural vegetation in these areas appears to have evolved a low structural profile whose height may not be dictated by grazing; plant growth may be restricted instead by flooding and saline conditions. This habitat specialization, in contrast to the more general habitat use exhibited by other upland shorebirds (RBL et al. unpubl. data), may have led the Buff-breasted Sandpiper to evolve high site fidelity, which may explain the large aggregations observed in some of these areas. Until more is known about the dependency of Buff-breasted Sandpipers on these unique habitats, care must be taken to monitor and preserve these areas.

The absence of Buff-breasted Sandpipers from many areas within Argentina that appeared to have suitable vegetation cover suggests that the landscape (e.g., spatial arrangement of wetlands and grasslands) or other environmental conditions (e.g., soil moisture and

compaction, fire frequency) may be inappropriate for the species. Alternatively, the species may exhibit high site fidelity to particular wintering sites, making these sites especially critical for protection. Observations across years from Estancia Medaland (Isacch and Martínez 1999; JPI unpubl. data) and Bahía Samborombón (DEB and M. Beade unpubl. data) in Argentina, Laguna de Rocha, and Laguna de Castillos in Uruguay (this study), and Banhado do Taim, Ilha do Torotama, and Lagoa do Peixe in Brazil (Resende and Leeuwenberg 1987; this study; GAB, JBA, and RAD unpubl. data), suggest particular wintering sites are used consistently from year to year. It also is possible that the available winter habitat in Argentina greatly surpasses the land needed by the current number of Buff-breasted Sandpipers, and factors away from the wintering grounds are preventing the species from increasing to previous levels.

Future research needs.—Additional research is needed on the wintering grounds to determine whether the distribution and abundance of Buff-breasted Sandpipers detected in our study is representative, or whether these patterns are likely to vary among years or with changes in weather patterns and economic conditions. Additional information on site tenacity, and local and regional movements within the wintering grounds, would help interpret our survey results and indicate the relative importance of sites with high numbers of birds. Further surveys on the species main wintering range would provide valuable trend information, and surveys where Buff-breasted Sandpipers are seen occasionally during winter (e.g., Puna Ecoregion in western Argentina and southern Bolivia, and the Rio Grande do Sul's central trough in Brazil) would help document the importance of these areas on a regional and national level. A study of the restricted coastal areas in Uruguay and Brazil is needed to determine if livestock grazing affects these native grasslands or whether the composite plant species are structurally stunted due to flooding, high salinity, or poor soil conditions. Such a study would be appropriate for Lagoa do Peixe National Park where such grasslands exist and cattle are slated for removal in the near future.

Currently, we are using satellite imagery and image analysis software to determine the amount of suitable habitat within the main wintering range in Argentina, Uruguay, and Brazil. We then will extrapolate population density estimates for each country to the suitable habitat area (stratified by quality) to generate an overall population estimate for the species. This estimate is crucial for determining the conservation status of the species.

Besides pasturelands, Buff-breasted Sandpipers relied on old and new rice fields in Brazil and Uruguay. These areas may expose the species to herbicides and pesticides. Indeed, RAD and M. I. Burger (unpubl. data) found that Buff-breasted Sandpipers and other Nearctic waders used rice fields at a time when agrochemicals were being applied aerially. Three adult Buff-breasted Sandpipers died from feeding on planted rice seeds treated illegally with Furadan 4F in Texas in 1983 (Flickinger et al. 1986), and pesticide exposure has been implicated in the decline of other upland species (e.g., Upland Sandpipers, *Bartramia longicauda*) in South America (White 1988). Natural grasslands in the Río de La Plata Grassland are being plowed increasingly and replaced by sown pastures supplemented with fertilizers and other agrochemicals (Oesterheld 1993). These practices also are economically driven and may change across years. Buff-breasted Sandpipers also may be exposed to agrochemicals along their migration route in the U.S. Here the species frequents altered habitats such as golf courses, sod fields, airport runways, cemeteries, and newly planted rice fields that are subject to herbicide and pesticide applications (Gotthardt and Lanctot 2002).

Virtually no information is available on the species migration in South America. Research is needed to determine if important regional stopover sites exist (e.g., Bahía de Asunción, Lesterhuis and Clay 2001) so they can be protected and included in the Western Hemisphere Shorebird Reserve Network (WHSRN 1993). This will require the cooperation of biologists in many countries and a concerted effort to look for this species during spring and fall migration. We are hopeful that the WHSRN, which identifies and gives protection to stopover sites used by migratory shorebirds in the Americas, will facilitate this. Research in the U.S. and Canada, where the species migrates and breeds, also may be needed

to determine if the species' decline is occurring because of problems during other parts of their annual cycle (see above). We are optimistic that the recent listing of the species in the U.S. (Brown et al. 2001) and Canadian (Donaldson et al. 2000) shorebird conservation plans will spur international cooperation toward these ends.

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APPENDIX. Buff-breasted Sandpiper records in South America from 1822 to 2000. See Figures 1 and 2 for locations of map numbers. Names and coordinates taken from ornithological gazetteer for each country when not provided by original reference (see Paynter 1982, 1985, 1989; Paynter and Traylor 1977, 1981, 1991; Paynter et al. 1975; Rand and Paynter 1981; Stephans and Traylor 1983, 1985). Observations are ordered by country and then latitude.

Map location	Country	Province/state/ department	Locality	Latitude	Longitude (W)
1	Argentina	Buenos Aires	Isla Bermejo-Bahía Blanca	S 39° 01′	62° 01′
2	Argentina	Buenos Aires	General Daniel Cerri	S 38° 42′	62° 24′
3	Argentina	Buenos Aires	Albufera Mar Chiquita	S 37° 38′	57° 24′
4	Argentina	Buenos Aires	Estancia Medaland	S 37° 26′	57° 10′
5	Argentina	Buenos Aires	Guaminí (near)	S 37° 02′	62° 25′
6	Argentina	Buenos Aires	Camino Real Viejo-La Isolina	S 36° 35′	56° 56′
7	Argentina	Buenos Aires	Camino Estancia El Palenque	S 36° 33′	56° 56′
8	Argentina	Buenos Aires	General Conesa	S 36° 31′	57° 20′
9	Argentina	Buenos Aires	Estancia El Tuyú	S 36° 31′	56° 46′
10	Argentina	Buenos Aires	Cañada "El Palenque"	S 36° 29′	56° 59′
11	Argentina	Buenos Aires	Canal Sta. Clara	S 36° 24′	57° 15′
12	Argentina	Buenos Aires	Canal 1	S 36° 26′	57° 17′
13	Argentina	Buenos Aires	Route No. 11 (Gral. Conesa - Gral. Lavalle)	S 36° 30′	57° 16′
14	Argentina	Buenos Aires	General Lavalle	S 36° 24′	56° 57′
15	Argentina	Buenos Aires	Punta Rasa	S 36° 19′	56°46′
16	Argentina	Buenos Aires	Dolores	S 36° 20′	57° 45′
17	Argentina	Buenos Aires	Rosas - FCS	S 35° 58′	58° 56′
18	Argentina	Buenos Aires	Bahía Samborombón	S 36° 00′	57° 20′
19	Argentina	Buenos Aires	Laguna las Flores Grande	S 35° 35′	59° 02′
20	Argentina	Buenos Aires	Pipinas	S 35° 32′	57 ° 20′
21	Argentina	Buenos Aires	Chascomús	S 35° 27′	57° 45′
22	Argentina	Buenos Aires	San Miguel Monte	S 35° 27′	58° 47′
23	Argentina	Buenos Aires	Camino Punta Indio Verónica	S 35° 17′	57° 15′
24	Argentina	Buenos Aires	San Vicente	S 35° 01′	58° 25′
25	Argentina	Buenos Aires	Estancia Plátanos	S 34° 47′	58° 11′
26	Argentina	Buenos Aires	Barracas al Sud	S 34° 39′	58° 22′
27	Argentina	Buenos Aires	Moreno	S 34° 39′	58° 48′
28	Argentina	Buenos Aires	Río Luján	S 34° 34′	59° 06′
29	Argentina	Buenos Aires	Bañados Río Arrecifes	S 33° 44′	59° 34′
30	Argentina	Entre Ríos	Ceibas	S 33° 26′	58° 45′
31	Argentina	Santa Fe	Maciel	S 32° 27′	60° 54′
32	Argentina	Santa Fe	Monje	S 32° 21′	60° 56′
33	Argentina	Santa Fe	Arocena	S 32° 05′	60° 58′
34	Argentina	Entre Rios	Paso de la Laguna	S 31° 49′	59° 10′
35	Argentina	Córdoba	Laguna Mar Chiquita	S 30° 54′	62° 40′
36	Argentina	Córdoba	Campo de Mare	S 30° 49′	62° 54′
37	Argentina	Córdoba	Terraplén Bañados Río Dulce	S 30° 15′	62° 20′

APPENDIX. EXTENDED

Map location	Count[a]	Month[b]	Year	Reference[c]
1	7, 7	10, 12	1991	Belenguer et al. 1992
2	6	12	1994	Delhey et al. 2001
3	present	??	??, 1982	Chani 1986, M. Martínez pers. comm.
4	4, 11, 14, 68, 262, 2000	1, 11, 12	1974, 1992, 1993	Myers and Myers 1979, Blanco et al. 1993
5	small flocks	3	1921	Wetmore 1927
6	50	12	1996	R. Fraga pers. comm.
7	1, 2, 6, 30	1, 10, 12	1987, 1988	Blanco et al. 1988, C. Laredo pers. comm., M. Rumboll pers. comm.
8	1, 3, 4	10	1987, 1992	Blanco et al. 1993, C. Laredo pers. comm., F. Moschione pers. comm.
9	2	10	1992	Blanco et al. 1993
10	present, 5, 18	1, 2	1987, 1989, 1992	Wetlands International, DEB unpubl. data, C. Laredo pers. comm., R. Stranek pers. comm.
11	3, 8, 15	10, 12	2000	DEB unpubl. data
12	5	12	2000	DEB unpubl. data
13	50	12	2000	DEB unpubl. data
14	1, 2, 7, 10, 22, 23, 53 and 1 skin	3, 10, 11	1902, 1920, 1992, 1993	Wetmore 1927, Blanco et al. 1993, MACN Collection, M. Babarskas pers. comm.
15	present	3	1994	A. Di Giacomo pers. comm.
16	38	3	1993	Blanco et al. 1993
17	2 skins	2	1926, 1927	MACN Collection
18	present	??	1993	Vila et al. 1994
19	30	spring	1972	C. Laredo pers. comm., J. Rodríguez Mata pers. comm.
20	8, 39	3, 12	1992, 1993	Blanco et al. 1993
21	present, 4	2, 3	1866, 1993	Dabbene 1920, Blanco et al. 1993
22	53	3	1993	Blanco et al. 1993
23	6	10	1989	C. Laredo pers. comm., F. Moschione pers. comm.
24	1	??	??	T. Narosky pers. comm.
25	present, 1 skin	3	1914, 1916	Dabbene 1920, MACN Collection
26	present, 1 skin	6, 12	1899, 1901, 1904	Dabbene 1920, FML and MACN Collections
27	1 skin	2	1876	Dabbene 1920, BM(NH) Collection
28	present	2	??	Hellmayr and Conover 1948
29	1 skin	3	1915	MACN Collection
30	1	2	1989	E. Abadie pers. comm.
31	few	3	1989	C. Laredo pers. comm., M. de la Peña pers. comm.
32	small group	5	1985	M. de la Peña pers. comm.
33	some	3	1986	de la Peña 1988
34	18	1	1992	C. Laredo pers. comm.
35	1	4	1978	Nores et al. 1983
36	2	12	1992	Blanco et al. 1993
37	13	2	1993	Wetlands International unpubl. data

APPENDIX. CONTINUED

Map location	Country	Province/state/department	Locality	Latitude	Longitude (W)
38	Argentina	Corrientes	Estancia Curipicay	S 29° 14′	57°56′
39	Argentina	Corrientes	Estancia San Juan Poriahu	S 27° 42′	57°11′
40	Argentina	Formosa	Misión Tacaaglé	S 24° 58′	58°47′
41	Argentina	Formosa	Las Lomitas (25 km South-southwest)	S 24° 43′	60°36′
42	Argentina	Jujuy	Laguna Guayatayoc	S 23° 23′	65°52′
43	Argentina	Jujuy	Laguna Río Miraflores	S 23° 02′	65°52′
44	Argentina	Jujuy	Laguna Runtuyoc	S 22° 39′	65°41′
45	Argentina	Jujuy	Laguna Vilama	S 22° 36′	66°45′
46	Argentina	Jujuy	Laguna Cangrejillos	S 22° 24′	65°34′
47	Argentina	Jujuy	Laguna de los Pozuelos	S 22° 21′	66°00′
48	Argentina	Jujuy	Cieneguilla	S 22° 05′	65°53′
49	Bolivia	Tarija	Lagunas de Tajzara	S 21° 42′	65°02′
50	Bolivia	Santa Cruz	Buena Vista	S 17° 27′	63°40′
51	Bolivia	El Beni	Tumi Chucua	S 11° 08′	66°10′
52	Bolivia	El Beni	Riberalta	S 10° 59′	66°06′
53	Bolivia	Pando	Victoria	S 10° 59′	66°10′
54	Brazil	Rio Grande do Sul	Arroio Taim mouth	S 32° 34′	52°35′
55	Brazil	Rio Grande do Sul	Estação Ecológica do Taim	S 32° 33′	52°35′
56	Brazil	Rio Grande do Sul	Granja Quatro Irmãos	S 32° 14′	52°29′
57	Brazil	Rio Grande do Sul	Praia do Cassino	S 32° 11′	51°14′
58	Brazil	Rio Grande do Sul	Lagoa dos Patos mouth	S 32° 10′	52°10′
59	Brazil	Rio Grande do Sul	Rio Grande	S 32° 02′	52°06′
60	Brazil	Rio Grande do Sul	Banhado do Pontal da Barra	S 31° 47′	52°14′
61	Brazil	Rio Grande do Sul	Bojuru Lighthouse surroundings	S 31° 26′	51°17′
62	Brazil	Rio Grande do Sul	Banhado Capão da Areia	S 31° 20′	51°09′
63	Brazil	Rio Grande do Sul	Lagoa do Peixe	S 31° 18′	51°00′
64	Brazil	Rio Grande do Sul	Rio Santa Maria	S 30° 15′	54°55′
65	Brazil	Rio Grande do Sul	Rio Jacuí	S 30° 03′	52°52′
66	Brazil	Rio Grande do Sul	Pólo Petroquímico, Triunfo	S 29° 56′	51°43′
67	Brazil	Rio Grande do Sul	Tramandaí (5 km northeast)	S 29° 56′	50°06′
68	Brazil	Rio Grande do Sul	Rio Ibirapuitã	S 29° 45′	55°46′
69	Brazil	Rio Grande do Sul	Vacaria surroundings	S 28° 30′	50°56′
70	Brazil	Paraná	Balneário Atami	S 25° 36′	48°23′
71	Brazil	Paraná	Pontal do Sul	S 25° 35′	48°22′
72	Brazil	São Paulo	Lagoa do Portão, Ipanema	S 23° 26′	47°36′
73	Brazil	Mato Grosso	Campos do Encanto, Vila Bela da Santíssima Trindade	S 15° 03′	59°44′
74	Brazil	Mato Grosso	Vila Bela da Santíssima Trindade	S 15° 00′	59°57′
75	Brazil	Acre	Plácido de Castro	S 10° 20′	67°11′
76	Brazil	Acre	São João	S 09° 09′	72°40′
77	Brazil	Rondônia	Porto Velho	S 08° 46′	63°54′
78	Brazil	Amazonas	Borba	S 04° 24′	59°35′
79	Brazil	Maranhão	Baixada Maranhense	S 03° 28′	44°53′
80	Brazil	Amazonas	Tefé Airport	S 03° 22′	64°25′
81	Brazil	Roraima	Boa Vista Airport	N 02° 49′	60°40′

APPENDIX. CONTINUED, EXTENDED

Map location	Count[a]	Month[b]	Year	Reference[c]
38	flock	??	1973	J. Hutton pers. comm.
39	2	9	1997	R. Fraga pers. comm.
40	2 skins	11	1925	Munchen Museum, cited in Laubmann 1930
41	1	1	1992	C. Laredo pers. comm., F. Moschione pers. comm.
42	2, 3, 5	2, 11	1992, 1993	C. Laredo pers. comm.
43	1	9	1991	Laredo 1996
44	12, 16, 23	1, 2, 12	1992, 1993	C. Laredo pers. comm.
45	9	9	1991	Laredo 1996
46	8, 15	1, 11	1992, 1993	C. Laredo pers. comm.
47	5, 7, 10, 13, 14, 19	1–3, 9, 12	1989, 1991–1993	Laredo 1996, C. Laredo pers. comm.
48	3, 5, 13	2, 3, 12	1988, 1992, 1993	Narosky 1988, C. Laredo pers. comm.
49	7	3	1992	C. Laredo pers. comm.
50	2 skins	10	1916	MACN and CM Collections
51	1 skin	10	1972	LSUMZ Collection
52	1, 2	9, 10	1937	Gyldenstolpe 1945
53	2	10	1937	Glydenstolpe 1945
54	3	2	1995	Wetlands International unpubl. data
55	??, hundreds	9–12, 1–3	1982, 1990–1992	Mähler et al. 1996, Voss 1990
56	10, 12, 1	10–12	1998	RAD unpubl. data
57	16	2	1995	Wetlands International unpubl. data
58	19	??	??	A. Witeck pers. comm.
59	1 skin	??	<1899	von Ihering 1899
60	range 1–32	1, 2, 9–12	1994	G. Maurício pers. comm.
61	10	9	1998	G. Maurício and GAB unpubl. data
62	16, 68	9	1998	G. Maurício and GAB unpubl. data
63	1, 1, 1, 5, 110, 200	1, 3, 4, 10	1972, 1974, 1988, 1997	Resende and Leeuwenberg 1987, WHSRN 1993, C. Laredo pers. comm., P. Collins and R. Jessop pers. comm., MN and MCN collections
64	28	1	1992	C. Laredo pers. comm.
65	22	1	1992	C. Laredo pers. comm.
66	4	10	1989	Belton 1994
67	1	8	1973	MCN Collection
68	13	1	1992	C. Laredo pers. comm.
69	3	8	1975	Belton 1994
70	alone/pairs	9	1993	Bornschein et al. 1997
71	alone/pairs, 2 skins	9–11	1993	Bornschein et al. 1997, MN Collection
72	present	11	1822	von Pelzeln 1870
73	2	11	2000	J. F. Pacheco pers. comm.
74	present	10	1826	von Pelzeln 1870
75	1 skin	9	1951	Pinto and de Camargo 1954, MZUSP Collection
76	5	8	1997	J. F. Pacheco pers. comm.
77	1	11	1954	Pinto 1964, MZUSP Collection
78	present	4	1830	von Pelzeln 1870
79	present	11	1985	Roth and Scott 1987
80	1	9	1994	J. F. Pacheco pers. comm.
81	3	9	1987	Stotz et al. 1992

APPENDIX. CONTINUED

Map location	Country	Province/state/department	Locality	Latitude	Longitude (W)
82	Brazil	Amazonas	Marabitanas	N 00° 58′	66° 51′
83	Brazil	Amazonas	Tapurucuará	S 00° 24′	65° 02′
84	Colombia	Antioquía	Remedios	N 07° 02′	74° 41′
85	Colombia	Meta	Hacienda Mozambique (near)	N 04° 00′	73° 02′
86	Colombia	Cauca	Popoyán	N 02° 27′	76° 36′
87	Colombia	Meta	Hacienda La Corocora	N 03° 16′	73° 03′
88	Colombia	Magdalena	Ciénaga	N 11° 01′	74° 15′
89	Ecuador	Napo/Pichincha	Volcan (Cerro) Antisana	S 00° 30′	78° 08′
90	Ecuador	Napo	Limóncocha	S 00° 25′	76° 38′
91	Ecuador	Pichincha	Carapungo	S 00° 09′	78° 22′
92	Ecuador	Imbabura	Hacienda Paramba	N 00° 49′	78° 21′
93	Paraguay	Central	Bahía de Asunción	S 25° 20′	57° 35′
94	Paraguay	Boquerón	Villa Hayes (320 km Northwest)	S 22° 47′	59° 57′
95	Paraguay	Presidente Hayes	Puerto Pinasco (west of)	S 22° 43′	57° 50′
96	Paraguay	Presidente Hayes	Estancia Campo María (Laguna Salada)	S 22° 32′	59° 18′
97	Paraguay	Presidente Hayes	Laguna Capitán	S 22° 32′	49° 41′
98	Paraguay	Alto Paraguay	Bahía Negra	S 20° 14′	58° 10′
99	Paraguay	Alto Paraguay	Estancia Doña Julia	S 20° 07′	58° 05′
100	Peru	Cuzco	Cosñipata	S 13° 04′	71° 11′
101	Peru	Madre de Dios	Río Manu and Río Madre de Dios (near Boca Manu)	S 12° 15′	70° 50′
102	Peru	Madre de Dios	Río Manu	S 12° 16′	70° 51′
103	Peru	Ucayali	Balta	S 10° 08′	71° 13′
104	Peru	Ucayali	Pucallpa (59 km west)	S 08° 24′	75° 12′
105	Peru	Loreto	Chamicuros	S 05° 30′	75° 30′
106	Peru	Loreto	Jeberos [or Xeberos]	S 05° 17′	76° 13′
107	Peru	Loreto	Iquitos	S 03° 46′	73° 15′
108	Peru	Amazonas	Orosa	S 03° 26′	72° 08′
109	Peru	Loreto	Pebas	S 03° 20′	71° 49′
110	Peru	Loreto	Isla de Iquitos	N 03° 43′	73° 12′
111	Suriname	Unknown province in coastal zone	Coastal inland wetlands (sector VI)	~N 05° 06′	~54° 55′
112	Suriname	Commewijne	Mariënburg	N 05° 53′	55° 03′
113	Uruguay	Maldonado	Balneario Solís	S 34° 48′	55° 22′
114	Uruguay	Maldonado	San Carlos	S 34° 48′	54° 55′
115	Uruguay	San José	Playa Penino	S 34° 45′	56° 25′
116	Uruguay	Canelones	Laguna (Cañada) del Cisne	S 34° 44′	55° 50′
117	Uruguay	Rocha	Balneario Las Garzas	S 34° 44′	54° 24′
118	Uruguay	Rocha	Laguna de Rocha and Arroyo La Palma	S 34° 33′	54° 11′
119	Uruguay	Rocha	Laguna de Rocha (mouth)	S 34° 31′	54° 22′
120	Uruguay	Rocha	Refugio Laguna Castillos	S 34° 20′	53° 55′

APPENDIX. CONTINUED, EXTENDED

Map Location	Count[a]	Month[b]	Year	Reference[c]
82	present	3	1831	von Pelzeln 1870
83	4	3	1963	MPEG Collection
84	1	2	1905	BM(NH) Collection
85	sightings	2	??	Hilty and Brown 1986
86	uncommon	12	??	Hilty and Brown 1986
87	c. 500	2, 3	1977	Hilty and Brown 1986
88	2 skins	9	1898	AMNH Collection, Hellmayr and Conover 1948
89	2 skins	9	1991	ANSP Collection
90	1	9	1976	LSUMZ Collection
91	present	7	??	Hellmayr and Conovor 1948
92	1 skin	4	1889	AMNH Collection, Hellmayr and Conover 1948
93	Range = 1–140, n = 60, mean = 4.8 and 11.9 in 80's and 2000, respectively	1–4, 9–12	1987–1989, 2000	Hayes and Fox 1991, Hayes et al. 1990, A. Hivekovics and R. Clay pers. comm.
94	2 skins	9	1973	MVZ Collection, cited in Hayes et al. 1990
95	1 and 1 skin	4, 9	1920, 1931	Wetmore 1927, AMNH Collection
96	6	9, 11	2000	R. Clay pers. comm.
97	5	10	2000	R. Clay pers. comm.
98	1	9	1997	R. Clay pers. comm.
99	i skin	9	1984	Hayes et al. 1990, MNHNP Collection
100	1 skin	9	1868	BM(NH) Collection
101	present	8–10	??	B. Walker pers. comm.
102	3, 3	10, 11	1983, 1989	Bolster and Robinson 1990, Begazo 1990
103	1	9	1964	LSUMZ Collection
104	1 skin	10	1971	AMNH Collection
105	2 skins	9	1867	BM(NH) Collection
106	1 skin	10	1866	BM(NH) Collection
107	4 skins	9	1878	Hellmayr and Conover 1948, BM(NH) and SMF Collections
108	12 skins	9	1926	AMNH, ANSP, and FML Collections, Bond 1955
109	1 skin	8	1866	Hellmayr and Conover 1948, BM(NH) Collection
110	1 skin	9	1985	ANSP Collection
111	tens to maximally a few hundreds	9–11, 3–5	1967, 1975	Jong and Spaans 1984
112	present, 1, 2 and skin(s?)	5, 8–11	1963, 1966–1969	Leiden Museum, cited in Haverschmidt 1972
113	present	2	1969	Gore and Gepp 1978
114	>80	3	1975	Gore and Gepp 1978
115	1 skin	11	1960	MNHNM Collection
116	6 skins	9, 10	1952, 1958	MNHNM Collection
117	1 skin	??	1959	MNHNM Collection
118	31, 40, 143, 216, 225	2, 11	1991–1993	Devesa et al. 1992, Blanco et al. 1993, Wetlands International unpubl. data
119	47, 164	1	1992	Wetlands International unpubl. data
120	35	2	1993	Wetlands International unpubl. data

APPENDIX. CONTINUED

Map location	Country	Province/state/ department	Locality	Latitude	Longitude (W)
121	Uruguay	Rocha	Laguna Negra and Bañado Santa Teresa	S 34° 00′	53° 45′
122	Uruguay	Rocha	Bañado de las Maravillas	S 33° 55′	53° 35′
123	Uruguay	Rocha	Bañado de los Indios	S 33° 55′	53° 45′
124	Venezuela	Dependencia Federal	Isla Gran Roque, Parque Nacional Archipelago de Los Roques	N 11° 58′	66° 40′
125	Venezuela	Falcón	Boca de Mangle, San Juan de los Cayos	N 11° 09′	68° 23′
126	Venezuela	Zulia	Lagunillas	N 10° 08′	71° 16′
127	Venezuela	Apure	Hato El Cedral	N 07° 25′	69° 19′
128	Venezuela	Amazonas	San Fernando de Atabapo	N 04° 03′	67° 28′
129	Venezuela	Amazonas	Simarawochi, Alto Río Metacuni	N 03° 49′	64° 36′
130	Venezuela	Amazonas	Culebra, Rio Cunucunuma	N 03° 44′	65° 45′
131	Venezuela	Amazonas	La Esmeraldo	N 03° 25′	65° 40′
132	Venezuela	Amazonas	El Merey, Caño Casiquiare	N 03° 05′	65° 55′
133	Venezuela	Amazonas	Misión Ocamo	N 02° 47′	65° 12′

[a] Individual counts are listed where possible, otherwise more general indications of the number of birds is given. "Skin" refers to a study skin in a museum collected from this locality.

[b] January = 1, February = 2, etc.

[c] Abbreviations for museums include Academy of Natural Sciences of Philadelphia (ANSP), American Museum of Natural History (AMNH), Carnagie Museum of Natural History (CM), Field Museum of Natural History, Chicago (FMNH), Forschungsinstitut Senckenberg, Frankfurt am Main (SMF), Fundación Miguel Lillo (FML), Louisiana State University Museum of Natural Science (LSUMZ), Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), Museo Nacional de Historia Natural de Montevideo (MNHNM), Museo Nacional de Historia Natural del Paraguay (MNHNP), Museu de Ciências Naturais (MCN), Museu de Zoologia da Universidade de São Paulo (MZUSP), Museu Nacional (MN), Museu Paraense Emilio Goeldi (MPEG), Museum of Vertebrate Zoology (MVZ), and The Natural History Museum (BM(NH)). Museum contacts are listed in the acknowledgments.

APPENDIX. CONTINUED, EXTENDED

Map location	Count[a]	Month[b]	Year	Reference[c]
121	9	1	1992	Wetlands International 1999
122	17, 210	1, 7	1991, 1992	Wetlands International 1999
123	40	1	1992	Wetlands International 1999
124	2	10	2000	D. Ascanio pers. comm.
125	3 skins	9	1966	Estación Biológica Rancho Grande Collection
126	3 (2 collected)	5	1920	Phelps and Phelps 1958, FMNH Collection
127	23, 32, 200	4, 5	2000	A. Chartier pers. comm., G. Rodríguez pers. comm., D. Willis pers. comm.
128	7 skins	3	1943	Phelps and Phelps 1958, W. H. Phelps Collection
129	1 skin	4	1972	W. H. Phelps Collection
130	1 skin	3	1983	W. H. Phelps Collection
131	4 skins	3	1929	AMNH Collection
132	1 skin	4	1929	AMNH Collection
133	1 skin	4	1978	W. H. Phelps Collection

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EFFECTIVENESS OF NEST TREATMENTS ON TICK INFESTATIONS IN THE EASTERN BROWN PELICAN

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ABSTRACT.—This study examined the effectiveness of treating ticks (*Ornithodoros capensis*) infesting nests of Eastern Brown Pelicans (*Pelecanus occidentalis carolinensis*). The number of immature ticks on nestling pelicans was significantly less in treated than in control nests. Nest abandonment also was less in treated nests; however, in severely infested nests, treatments did not prevent abandonment. Nesting success and hematocrit measurements did not differ significantly between control and treated groups. *Received 13 November 2000, accepted 22 March 2002.*

Colony abandonment associated with excessive tick infestations is one factor that continues to negatively impact the reproductive success of Brown Pelicans (*Pelecanus occidentalis*; Terrence et al. 1985; Duffy 1983; King et al. 1977a, 1977b). Large colonies of nesting seabirds provide ticks and other parasites with a readily available supply of hosts for food, shelter, and reproduction (Duffy 1988). Ticks survive year round in nest cores and reused nesting material, which subsequently provide ticks access to a dependable food source in following years (Humphrey-Smith and Moorhouse 1981). This relationship may provide both immediate and long term negative impacts on the host population of nesting birds. Ectoparasites can cause brood mortality (Feare 1976, Chapman and George 1991), nest abandonment (Duffy 1983; King et al. 1977a, 1997b), and reduced fitness, as evidenced by slowed development and reduced hematocrit levels in colonies of Cliff Swallows (*Petrochelidon pyrrhonota*; Chapman and George 1991). Boulinier and Danchin (1996) suggested that the effects of tick infestation on the reproductive success of Black-legged Kittiwakes (*Rissa tridactyla*) may affect recruitment and breeding site fidelity, and consequently impact trends in host populations.

Nest abandonment is perhaps one of the most damaging effects of ticks. During 1975, Brown Pelicans nesting at Aransas National Wildlife Refuge in Texas abandoned nests before hatching. Subsequent inspections revealed large populations of ticks in the nests and surrounding area; these were *Ornithodoros capensis*, reported only once previously in the continental United States (King et al. 1977a). Brown Pelicans in California infested with the tick *O. denmarki* experienced years of low productivity associated with abandonment of eggs and young (King et al. 1977b).

In the southeastern United States, tick infestations have been linked to nest desertions of Eastern Brown Pelicans (*Pelecanus occidentalis carolinensis*) in North and South Carolina. More than 90% of the nests were abandoned in a heavily infested colony at Bird Key Stono, South Carolina, during 1987 (Wilkinson et al. 1994). Desertion also occurred at Marsh Island in Berkeley County, South Carolina, again associated with tick infestations (Keirans et al. 1992). Wilkinson et al. (1994) first noted tick-associated desertion of 80 nests on an island in the Cape Fear River of North Carolina during 1991. *Ornithodoros capensis* was collected from colonies of Brown Pelicans on North Pelican Island and Ferry Slip Island in the Cape Fear River in 1991 (Keirans et al. 1992).

The objectives of this study were (1) to compare tick populations in Brown Pelican nests treated with pesticide to those in nests left untreated on South Pelican and Ferry Slip islands, (2) to determine if tick populations adversely impact nesting success, and (3) to determine if tick infestations reduce hematocrit levels in nestling Brown Pelicans.

STUDY AREA AND METHODS

South Pelican Island (33° 56′ N, 77° 53′ W) and Ferry Slip Island (33° 58′ N, 77° 56′ W) in the Cape

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Fear River of North Carolina served as study sites for this project. We selected nests at the beginning of the nesting season after egg laying began. During the 1998 season, nesting began in April. In 1999 pelicans began successfully nesting during May.

During 1998 we selected nests on each island by walking line transects across the island and alternately assigning nests as treated and control until we had a sample of 30 nests. Fifteen nests were treated with 1% diluted Rabon 50WP^{R}, a poultry spray that previously has been used to treat Brown Pelican nests in South Carolina (P. Wilkinson pers. comm.) and 15 nests were sprayed with tap water (control nests). We used garden spray containers to spray all nests, with spray directed underneath and around the eggs. We applied treatments twice during the incubation period during the 1998 nesting season and applied a third treatment on Ferry Slip Island approximately 1 week after chicks hatched, in an effort to obtain better tick control.

During the 1999 nesting season, we selected 60 nests on each island: 20 treated, 20 control, and 20 undisturbed (no application). Treated nests were sprayed with 0.5% Permectrin™ for the first two treatments, increased to 1% dilution for the third treatment to improve treatment effects. We applied three treatments on each island during the 1999 nesting season, two during incubation and one approximately 1 week after hatching. Control applications followed similar schedules during each season.

We monitored the number of eggs and chicks ≤2 weeks of age; chicks wander from the nest at 3–4 weeks of age. We visited each nest about once per week during 1998 and 2–3 times per week during 1999 to monitor nesting success. We considered those nests missing all eggs or with cold eggs and neither parent present to be abandoned. We calculated hatching success as the number of eggs hatched/eggs laid. We also calculated the number of young that survived to 2 weeks of age/number of young hatched. We calculated hatching success and percent surviving 2 weeks independently for each nest.

We examined each nestling in treated and control nests every 7–10 days following hatching for the presence of ticks; we did not examine nestlings on each visit to the colony in order to minimize disturbance. Counts of ticks and tick bites were restricted to the neck and beneath the wings of nestlings. We recorded tick infestations and nestling mortality for each nest until nestlings left the nesting area at approximately 3 weeks of age. We did not count ticks on nestlings in undisturbed nests.

We sampled blood from all nestlings in a subset of control and treated nests. Using a microhematocrit tube, we collected a drop of blood from the brachial vein. During 1998 we sampled nestlings approximately 1 week old from 10 control and 9 treated nests on South Pelican Island and from 10 control and 10 treated nests on Ferry Slip Island. During 1999 we sampled approximately 2-week-old nestlings from 8 control and 8 treated nests on each island.

During 1998 we collected nest material from all control, treated, and undisturbed nests on each island 2–4 weeks after chick departure. During 1999 we collected nest materials from abandoned nests immediately after noting abandonment and from all remaining nests 1–2 weeks after chick departure.

We placed nest materials in Berlese funnels (e.g., Bookhout 1994) positioned directly over 5-mm diameter jars containing 70% ethanol. Samples initially were heated from 48–72 h. Samples heated 48 h showed no difference in numbers of ticks collected relative to those heated 72 h, so all subsequent samples were heated 48 h. We then weighed the nest material to determine the number of ticks/kg dry weight. For those samples not run immediately, we placed a paper towel saturated in distilled water inside the plastic bag and stored the material in an incubator at 15° C until the samples were analyzed. We counted all ticks from each sample of nest material. Adult and nymph stages were not differentiated as both feed on pelicans and are distinguished only by the presence of a genital pore (Sonenshine 1991).

We compared control and treated nests separately by island and year. The number of ticks on nestlings was compared using the greatest mean number of ticks observed on all nestlings in a given nest over all dates (hereafter "tick intensity"). We compared hematocrit measurements for nestlings from control and treated nests using the mean for all chicks in the same nest. We tested the data for normality and data that did not meet normality criteria were analyzed using nonparametric statistics.

RESULTS

We never observed adult ticks on pelican nestlings. More immature ticks occurred on pelican nestlings in control nests than in treated nests. During 1998, tick intensity on nestlings ranged from 0–61. On South Pelican Island, mean tick intensity was 10.4 ± 3.7 SE ticks in control nests (n = 10) and 2.3 ± 1.2 SE ticks in treated nests (n = 12), a significant difference (Wilcoxon rank sums Z = 2.13, P = 0.03). On Ferry Slip Island, tick intensity was 12.6 ± 5.0 SE ticks in control nests (n = 12) and 1.7 ± 0.7 SE ticks in treated nests (n = 14; Z = 2.73, P = 0.006).

Whereas low levels of tick infestation occurred throughout 1998, tick numbers during 1999 were extremely low until mid-July, when the chicks reached approximately 2.5 weeks of age. At this time tick abundance increased markedly. Tick intensity during 1999 ranged from 0–100. On South Pelican Island, tick intensity was 20.1 ± 6.5 SE ticks in control nests (n = 11) and 4.2 ± 3.3 SE ticks in treated nests (n = 15; Z = 2.95, P = 0.003). On Ferry Slip Island, tick intensity was 12.8

± 5.3 SE ticks in control nests (n = 19) and 0.4 ± 0.2 SE ticks in treated nests (n = 19; Z = 4.08, $P < 0.0001$).

During 1998, no nest abandonment occurred in treated nests on either island whereas nest abandonment occurred in 40% of control nests on South Pelican Island (Pearson χ^2 = 7.5, df = 1, P = 0.01) and 27% of control nests on Ferry Slip Island (χ^2 = 4.6, df = 1, P = 0.03). During 1999 on South Pelican Island, two treated, three control, and three undisturbed nests were abandoned 2 weeks into the incubation period. Subsequent sampling revealed extremely high tick levels in these nests. There was no significant difference in abandonment among groups on South Pelican Island (χ^2 = 3.7 df = 2, P = 0.15) or Ferry Slip Island (χ^2 = 1.03, df = 2, P = 0.60).

During 1998, South Pelican Island control nests had a mean of 101.9 ± 62.0 SE ticks/kg nesting material and treated nests had a mean of 36.6 ± 12.8 SE ticks/kg (Wilcoxon rank sums Z = 0.0, P = 1.0). On Ferry Slip Island, control nests had a mean of 52.0 ± 28.5 SE ticks/kg and treated nests had 50.6 ± 15.7 SE ticks/kg (Z = 0.77, P = 0.44). During 1999, there was no significant difference in ticks/kg among undisturbed (mean = 81.4 ± 46.7 SE), control (mean = 70.7 ± 40.4 SE), and treated nests (mean = 44.1 ± 30.3 SE) on South Pelican Island (Kruskal-Wallis χ^2 = 2.71, df = 2, P = 0.26) or Ferry Slip Island (undisturbed: mean = 3.2 ± 0.9 SE; control: mean = 1.9 ± 0.5 SE; treated: mean = 2.4 ± 0.7 SE; χ^2 = 0.57, df = 2, P = 0.75). The series of abandoned nests on South Pelican Island ranged from 58–869 ticks/kg; consequently, these nests may have been infested with a total of 270–3910 ticks.

There were no significant differences in nestling hematocrit readings between control and treated groups during 1998 (mean hematocrit for South Pelican Island: 38.0% ± 1.3 SE for control nests and 39.3% ± 2.0 SE for treated nests, ANOVA F = 0.301, df = 18, P = 0.59; for Ferry Slip Island: 30.7% ± 1.6 SE for control nests and 31.1% ± 2.1 SE for treated nests, F = 0.031, df = 19, P = 0.86). There was a significant difference in hematocrit readings between islands (two-way ANOVA; Island: F = 8.83, df = 1, P = 0.005; Control/Treated: F = 0.26, df = 1, P = 0.61; there were no significant interactions: F = 0.05, df = 1, P = 0.82). During 1999, nestlings in control nests on South Pelican Island had a mean hematocrit of 38.3% ± 1.8 SE while those in treated nests had a mean of 38.6% ± 2.0 SE (ANOVA F = 0.016, df = 15, P = 0.90) and nestlings in control nests on Ferry Slip Island had a mean of 38.9% ± 1.4 SE while those in treated nests had a mean of 39.8% ± 2.4 SE (Wilcoxon rank sums Z = 0.26, P = 0.79).

Hatching success was similar for all groups on both islands during both years. During 1998, mean hatching success on South Pelican Island was 85.7% ± 6.7 SE for control nests (n = 7) and 88.9% ± 5.6 SE for treated nests (n = 9; Z = 0.31, P = 0.75) while mean hatching success on Ferry Slip Island was 86.7% ± 5.4 SE for control nests (n = 10) and 84.5% ± 6.2 SE for treated nests (n = 14; Z = 0.03, P = 0.97). During 1999, mean hatching success on South Pelican Island was 86.5% ± 4.6 SE for undisturbed nests (n = 16), 80.6% ± 6.4 SE for control nests (n = 12), and 79.2% ± 7.2 SE for treated nests (n = 16; Kruskal Wallis χ^2 = 0.538, P = 0.76) while mean hatching success was 84.2% ± 6.3 SE for undisturbed nests (n = 20), 88.6% ± 4.0 SE for control nests (n = 19), and 87.7% ± 5.1 SE for treated nests (n = 19; χ^2 = 0.066, P = 0.97).

There was no significant correlation between 2-week nest success and tick intensity during 1998 (Spearman r_S = −0.17, P = 0.30) or 1999 (r_S = −0.07, P = 0.61). Also during 1998, 2-week nest success did not differ significantly between control nests (90.5% ± 6.1 SE, n = 7) and treated nests (100%, n = 9) on South Pelican Island (Wilcoxon rank sums Z = 1.57, P = 0.12) or on Ferry Slip Island (control nests: 80.0% ± 6.9 SE, n = 10; treated nests: 81.0% ± 8.4 SE, n = 14; Z = 0.50, P = 0.62). There was a significant difference in total 2-week success between islands (Z = 2.04, P = 0.04). During 1999, mean 2-week success was 90.0% ± 4.5 SE for undisturbed nests (n = 15), 94.4% ± 3.7 SE for control nests (n = 12), and 93.3% ± 3.6 SE for treated nests (n = 15) on South Pelican Island (Kruskal Wallis χ^2 = 0.53, df = 2, P = 0.77) while mean 2-week success was 90.2% ± 3.8 SE for undisturbed nests (n = 17), 91.2% ± 4.3 SE for control nests (n = 19), and 90.4% ± 4.7 SE for treated nests (n = 19) on Ferry Slip Island (χ^2 = 0.236, P = 0.89).

DISCUSSION

During both 1998 and 1999, treatments effectively reduced the number of immature ticks infesting pelican nestlings, which suggests that nest treatments can control tick populations. Greater tick intensities were observed later in the season each year, but this was most obvious during 1999. While no visible ailments were apparent in chicks carrying large tick loads, the additional burden of ticks may further limit chick survival during years when other stresses affect reproduction. In addition, *Ornithodoros capensis* carries five different viruses (Yunker et al. 1979), although the effects of these on their hosts are largely unknown (Feare and Gill 1997).

In a similar study of *Argas* [*Persicargas*] *robertsi* infestation on Cattle Egrets (*Bubulcus ibis*), McKilligan (1996) observed a nesting season in which all chicks with tick loads exceeding 24 ticks/nestling subsequently died. Cattle egrets in infested nests experienced significantly greater mortality than those in treated nests (which were completely free of ticks) during the first season whereas no difference occurred during the second season. Tick loads were extremely variable within and between years, with much lower levels of infestation occurring during the second season. A similar pattern occurred in the present study, with some chicks having in excess of 100 ticks and many chicks having no ticks.

Our finding of no significant difference in hatching success or 2-week success among undisturbed, control, and treated nests suggests that the levels of nest infestation on the islands were not great enough to severely impact the nestlings. In contrast, Chapman and George (1991) recorded higher fledgling success from treated Cliff Swallow nests than from untreated nests. The swallow bug (*Oeciacus vicarius*) was the most abundant of four ectoparasites (three species of which were ticks) affecting these colonies. Richner et al. (1993) detected no differences in hatching success between nests with and without the hen flea (*Ceratophyllus gallinae*) in Great Tits (*Parus major*), although fledgling success was higher in nests free of these parasites.

Although we found no significant difference in the number of ticks collected from nests in undisturbed, control and treated nests, it is possible that ticks residing deep in the core of the nest were beyond reach of the pesticide. While examining infestations of *Ornithodorus amblus* in Guanay Cormorant (*Phalacrocorax bougainvillii*) nests in Peru, Duffy (1983) observed more ticks in the nest base than the nest cup. In addition, Duffy and Daturi (1987) observed strong diel patterns in the activity of *O. capensis*, in which the ticks were much more active during night than day. If adult ticks were deep within pelican nests when the treatments were applied, it is possible the treatment did not effectively reach those deep within the nest core. The treatments appeared to be much more effective on immature ticks, as would be expected because they reside closer to the nest surface.

Nest abandonment can play a large role in a colony's total reproductive success. Duffy (1983, 1988) described an abandonment "wave" that moved throughout a colony of Peruvian seabirds, which subsequently left eggs available to hungry gulls. For those nests containing chicks, subsequent mortality followed from exposure, starvation, or parasites. Similarly, King et al. (1977b) described nest abandonment as a gradual process moving through colonies of California Brown Pelicans and noted that abandonment was largely responsible for low reproduction in the Gulf of California during previous years. In our study, the severity of tick infestation in the abandoned nests and the progressive abandonment suggest that the abandonment was, at least in part, tick related.

In contrast to our study, ectoparasites significantly affected hematocrit levels in Cliff Swallows (Chapman and George 1991), Cattle Egrets (McKilligan 1996), and Great Tits (Richner et al. 1993). Wanless et al. (1997) observed that in Black-legged Kittiwakes, lower hematocrit values were related to higher tick levels, but in Common Murres (*Uria aalge*) they were not. Whereas tick loads in the present study did not appear to have adverse physiological effects, this nonetheless may occur in more severe infestations. W. Golder and J. Brunjes (pers. comm.) observed that infestations during past seasons in this study area have been much more severe as evidenced by red, irritated skin rashes on chicks. In such a situation, ticks may reduce chick fitness and

predispose chicks to adversities from other environmental stresses.

Wolf et al. (1985) recorded a mean hematocrit of 44.4% ± 1.1 in eight hatch-year captive Brown Pelicans. While this is higher than values measured in the present study, our hematocrits values were still above levels indicating anemia (>35%; Campbell and Morton 1984), with the exception of Ferry Slip Island during 1998. On Ferry Slip Island during 1998, hematocrit values were significantly lower in both control and treated nests. There are several possible explanations for this. First, higher temperatures can result in lower hematocrit readings (Kubena et al. 1972, Moye et al. 1969); the pelicans on Ferry Slip Island began nesting later, during warmer temperatures. Second, J. Brunjes (pers. comm.) noted that while food supplies appeared abundant at the beginning of the 1998 season, they appeared to decrease as the season progressed. Nesting on Ferry Slip Island during 1998 began approximately 4 weeks after South Pelican Island. It is possible that the lower hematocrit readings reflected the stresses from low food supplies. This also may explain the lower 2-week nesting success in both control and treated nests on Ferry Slip Island during 1998, as food supplies can significantly impact reproduction in Brown Pelicans (Anderson et al. 1982).

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ASSESSING EDGE AVOIDANCE AND AREA SENSITIVITY OF RED-EYED VIREOS IN SOUTHCENTRAL ONTARIO

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ABSTRACT.—We assessed edge avoidance, area sensitivity, and the relationship between local and regional forest cover for nesting Red-eyed Vireos (*Vireo olivaceus*) in 13 forest fragments (1–2,353 ha in size) in southcentral Ontario, Canada. Red-eyed Vireo territories and nests were not significantly farther from the edge than random points in any of the forest fragments, and there was no relationship between the probability of a male pairing and the distance of the territory from the edge of the forest fragment. The density of singing males and the probability of a male being paired increased significantly with increasing local forest cover within a 2-km radius of a study site, but not with forest fragment area or regional forest cover within a 10-km radius. Nest success was low and the probability of a nest being parasitized by the Brown-headed Cowbird (*Molothrus ater*) or successfully fledging ≥1 host young did not vary with distance of the nest from the forest edge or with any of our area or forest cover measures. Red-eyed Vireos did not display edge avoidance nor did they appear to be area sensitive within our study region, but there was a positive relationship with the amount of local (2-km radius) forest cover. Maintaining localized regions with high forest cover has been recommended on numerous occasions for the conservation of area sensitive species; our results suggest high forest cover also may benefit species that do not appear to be area sensitive. *Received 22 May 2001, accepted 17 April 2002.*

The Red-eyed Vireo (*Vireo olivaceus*) is a forest-dwelling Neotropical migrant songbird that breeds within deciduous and mixed forests throughout much of North America. At present, conclusions concerning the habitat requirements of this species are contradictory, particularly in regard to forest edge avoidance and minimum habitat requirements. Although not considered to be in decline (Sauer et al. 2001), habitat requirements of any species should be known before population declines are evident as the appropriate classification can influence future management of the species. Recent studies variously suggest that the Red-eyed Vireo avoids forest edges (reviewed in Villard 1998) or is an interior-edge generalist with extremely plastic habitat use, including wooded suburbs, fence rows, and forest edges (James 1976, Whitcomb et al. 1981). Most, but not all, studies suggest that the species is area sensitive (reviewed in Freemark and Collins 1992). None of the studies upon which these classifications are based include data from nest sites or reproductive success.

Edge avoidance has been defined by lower occurrences of territories and nests along the edge of a forest fragment than in the forest interior (King et al. 1997, Villard 1998). An area sensitive species is one that occurs more frequently, or increases in density, as fragment area increases (Freemark and Collins 1992). Area sensitive species should thus show positive relationships between the density of singing males and the area of forest fragments. Species with the greatest area sensitivity are presumed to show positive relationships between forest fragment area and male density, pairing success, and nesting success (e.g., Ovenbirds, *Seiurus aurocapillus*; Robinson et al. 1995, Burke and Nol 1998), so that the productivity (number of fledged young produced per ha of forest) of a forest fragment is very strongly influenced by forest fragment area. Recent studies also indicate that many forest bird species experience reduced density, pairing success, and nesting success in forest fragments embedded in regions with low forest cover (Robinson et al. 1995, Mazerolle and Villard 1999). Thus, forest habitat loss should negatively impact: (1) species that avoid forest edges, (2) species that are area sensitive, and (3) species that respond negatively to reduced amounts of forest cover. Establishing the appropriate classification for the Red-eyed Vireo (and other forest bird species) will help direct land use planning and forest conservation strategies.

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In this study, we tested whether Red-eyed Vireos nesting in forest fragments in deciduous woodlands of southcentral Ontario avoid edges, and whether male density, pairing success, and nesting success vary in relation to fragment size. Given the flexibility in habitat preferences reported for this species (James 1976) but the general restriction to wooded areas, we tested whether Red-eyed Vireos respond more strongly to forest cover or forest fragment area by determining which is the better predictor of male density, pairing success, and nesting success in our study area.

METHODS

Study area.—We conducted the study in eight forest fragments during 1997 and five during 1998, all situated in the Great Lakes-St. Lawrence Lowlands of southcentral Ontario, Canada (Hills 1959) near Peterborough, Ontario (44° 18′ N, 78° 19′ W). We selected fragments of upland deciduous forest to represent a wide range of fragment areas (1–2,352 ha). The surrounding landscape consisted of agriculture and rural low density housing (0–3 houses around the fragment perimeter).

Study plots, ranging from the entire forest in smaller fragments to 4-ha plots, were located within relatively mature (>40 years) deciduous, closed canopy forest. Plots within larger fragments were square in shape, with one edge located near the forest edge to allow comparison with small forest fragments. The vegetation of all study sites was dominated by mature sugar maple (*Acer saccharum*), but also included American beech (*Fagus grandifolia*), ironwood (*Ostrya virginiana*), and white ash (*Fraxinus americana*); less abundant canopy species included eastern hemlock (*Tsuga canadensis*), white elm (*Ulmus americana*), and white pine (*Pinus strobus*; Burke and Nol 2000).

We assessed the degree of habitat loss from fragment area and by three scales of forest cover: 2-km radius (1,260 ha), 5-km radius (7,850 ha), and 10-km radius (31,420 ha). Multiple scales were considered to gain a better understanding of the relationship between Red-eyed Vireo reproductive success and the amount of forested area in a region. We measured the surrounding forest cover from the center of the fragment using forest cover maps derived from LANDSAT imagery taken in 1984 and 1985 (Hounsell et al. 1992) and digitizing software. The area of the study fragment was excluded when measuring forest cover in order to reduce correlation between fragment area and surrounding forest cover.

Edge avoidance.—We assessed whether Red-eyed Vireos were avoiding edges by measuring the distance to the nearest nonforest edge from territories and nests, and comparing these to distances to the edge from randomly selected points within each forest fragment. We defined forest edge as any break in the canopy with a diameter ≥3 times the canopy height (Paton 1994). The distance from a territory to the nearest edge was measured from a song perch where a male had been observed singing. The number of random points per fragment varied from two in the smallest fragments to five (58 total). We analyzed these data using analysis of covariance (ANCOVA) with fragment size as the covariate and site (territory or nest versus random points) as the class variable. This design allows for a test of differences in the distance from territories and nests to the forest edge in comparison to the distance to the edge from random points while controlling for inherent differences in the distance to the edge as a function of fragment area (PROC GLM; SAS Institute, Inc. 1990). Fragment size and distance to the edge were log transformed to conform to the assumptions of ANCOVA.

Area sensitivity.—We determined the density of male Red-eyed Vireos within each fragment by spot mapping from early June to early July each year. Each fragment was visited 2–3 times per week during early morning and the locations of singing males were recorded. In larger fragments, not all territories occurred completely within the bounds of the plot. Males with the majority of a territory within the plot were given a value of 0.5 territory whereas birds with the majority of a territory occurring outside the plot were not included (Villard et al. 1993). We compared male density across the continuum of fragment sizes and forest cover measures using multiple regression (PROC GLM; SAS Institute, Inc. 1990).

To determine pairing success, we observed individual Red-eyed Vireo males throughout June and July. Mating status was determined by one or a combination of several criteria (Villard et al. 1993). Since male and female Red-eyed Vireos are not sexually dimorphic in appearance, we considered males to be paired if they were engaged in nonaggressive interactions with another bird of the same species. We also considered males paired if we observed them carrying food or feeding fledglings, or if we found an active nest within a territory. Gibbs and Faaborg (1990) and Villard et al. (1993) both suggested 90 min of total observation time is needed to conclude that ground nesting birds are not paired. However, because male Red-eyed Vireos were difficult to observe in the canopy, we extended this time; we visited each male repeatedly over the study period until there was positive proof of pairing or until approximately 120 min of total observation time had elapsed, at which time we assumed the bird was not paired. Each observation session continued until visual or auditory contact had ceased for ≥5 min.

We found nests by observing adult birds fly to the nest as well as systematically searching the foliage within territories. As nests situated on higher branches were more difficult to observe, it is possible that there was a bias toward finding lower nests. We checked each nest every 3–5 days and recorded nest contents. We considered a nest successful if ≥1 young of the host species fledged, and failed if no young of the host species fledged. We considered failed nests depredated if the nest structure, eggs, or nestlings disappeared, or parasitized if no host young fledged although Brown-

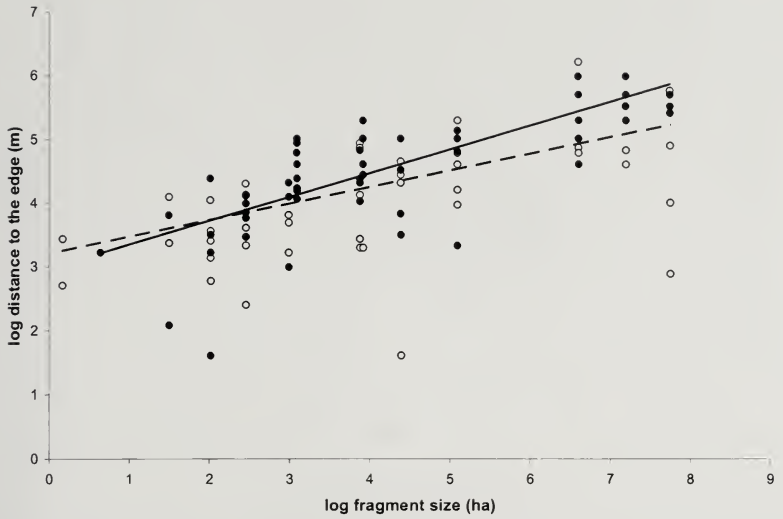

FIG. 1. Distance to the nearest nonforested edge from male Red-eyed Vireo territories (solid circles and solid line) and randomly located points (open circles and dashed line) across a continuum of fragment sizes for 13 forest fragments in southcentral Ontario, Canada, during the 1996 and 1997 breeding seasons.

headed Cowbird (*Molothrus ater*) young may have fledged successfully. As most parasitized nests successfully fledged host and cowbird young, we determined the proportion of nests containing cowbird eggs or young (parasitism rate).

We analyzed pairing and nesting success as a function of fragment size and forest cover measures using logistic regression (PROC LOGISTIC; SAS Institute, Inc. 1990). Distance from the edge was analyzed in separate logistic regressions to determine whether there was a significant relationship with the probability of pairing or nesting successfully. Logistic regression calculates the probability of obtaining a "success" as predicted by the independent variables (Manly 1994). Thus, each male Red-eyed Vireo was considered individually and defined as successful if paired. The probabilities of nest success, predation, and parasitism also were analyzed in this manner. Because forest fragments, rather than individual birds or nests, were the appropriate sample units, the dependent variable was considered as the proportion of successes to the total number in each fragment (events/trial syntax in the MODEL statement; SAS Institute, Inc. 1990:1079). All independent variables were log transformed to conform to the assumptions of logistic regression.

RESULTS

Data from 1997 and 1998 were combined because there were no significant differences between years in male densities (*t*-test: $t_{11} = 1.08$, $P = 0.30$), pairing success ($t_{11} = 1.86$, $P = 0.090$), or nesting success ($t_6 = 0.74$, $P = 0.48$). Forest cover within 2 km and 5 km were highly correlated ($r = 0.73$, $P = 0.003$) as was forest cover within 5 km and 10 km ($r = 0.87$, $P < 0.0001$) so we used only the 2 km (hereafter "local forest cover") and 10 km (hereafter "regional forest cover") measures of forest cover in the analyses ($r = 0.52$, $P = 0.070$). Forest fragment area was not correlated with either local ($r = 0.42$, $P = 0.15$) or regional ($r = 0.19$, $P = 0.52$) forest cover.

Edge avoidance.—We measured the distance to the nearest forest edge from 62 Red-eyed Vireo territories, 36 nests, and 58 randomly selected points. The overall model comparing the distance of territories and random sites was significant (ANCOVA: $r^2 = 0.47$, $F_{3,116} = 34.19$, $P = 0.0001$, $n = 13$ fragments). The significance of the model was driven by greater distances to the edge in larger forest fragments (size effect: $F_{1,116} = 94.55$, $P = 0.001$), as there was no trend for territories to be farther from the edge than random points (site effect: $F_{1,116} = 0.53$, $P = 0.47$; size × site interaction: $F_{1,116} = 2.89$, $P = 0.092$; Fig. 1). The overall model comparing distance to the edge from nests and random points was significant (ANCOVA: $r^2 = 0.15$, $F_{3,70} = 4.12$, $P = 0.010$, $n = 8$ fragments). Again, distances to the edge were greater in larger forest fragments and were not farther from the edge than randomly selected points (size effect: $F_{1,70} = 11.97$, $P = 0.0009$; site effect: $F_{1,70} = 1.64$, P

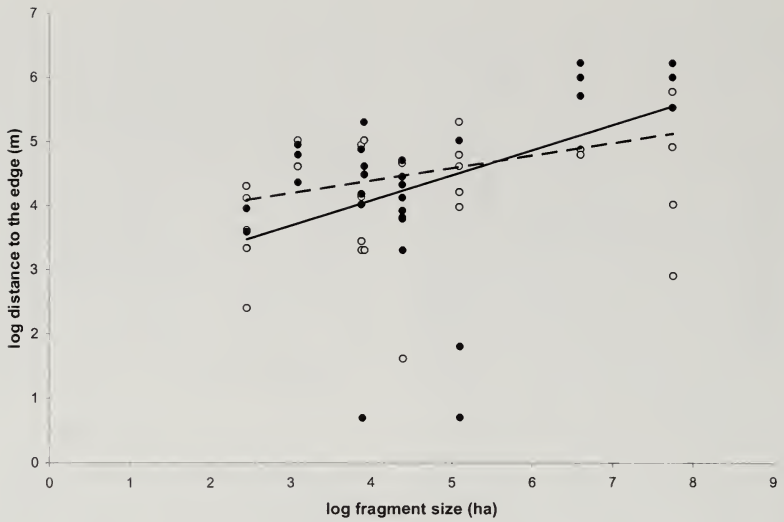

FIG. 2. Distance to the nearest nonforested edge from Red-eyed Vireo nests (solid circles and solid line) and randomly located points (open circles and dashed line) across a continuum of fragment sizes for eight forest fragments in southcentral Ontario, Canada, during the 1996 and 1997 breeding seasons.

= 0.20; fragment × site interaction: $F_{1,70}$ = 1.36, P = 0.25; Fig. 2). Before log transformation, the variability (SE) in distance to the nearest nonforest edge of territories, nests, and random points all increased significantly with forest fragment size (linear regression; territory: r_2 = 0.68, $F_{1,11}$ = 26.22, P = 0.0007; nest: r_2 = 0.77, $F_{1,6}$ = 25.07, P = 0.002; random: r^2 = 0.39, $F_{1,11}$ = 7.1, P = 0.015).

Area sensitivity.—Sites ranged in percent forested area from 11–94.3% at the local (2-km radius) forest cover scale and from 13.5–53.2% at the regional (10-km radius) forest cover scale. Red-eyed Vireos occurred in all 13 forest fragments, ranging in density from 0.7–4.7 males/ha. The overall regression model for predicting the density of male Red-eyed Vireos was significant (r^2 = 0.37, $F_{3,9}$ = 3.34, P = 0.050). Density increased significantly as a function of local forest cover (Fig. 3), but did not vary significantly with either fragment area or regional forest cover (Table 1).

We determined pairing success for 79 male Red-eyed Vireos; 46 (58.2%) were paired. Local forest cover was the only independent variable to enter significantly into the logistic regression model, indicating it was the best predictor of any individual male Red-eyed Vireo successfully attracting a mate (Table 2; Fig. 4). There was a significant positive correlation between density and pairing success (r = 0.8, P = 0.0006, n = 13 fragments).

Red-eyed Vireos build a hanging cup nest suspended from the fork of a small branch, ranging from 0.5–21 m in height but typically located from 2–4 m (Peck and James 1987). A total of 47 nests was found in eight forest fragments during the two years; 19 (40.4%) successfully fledged ≥1 host young. Neither forest area, local forest cover, regional forest cover, nor distance of the nest to the edge significantly affected the probability of nesting successfully (Table 2). Predation accounted for the majority of nest failures, with 25 nests (53.2%) depredated. Again, none of the independent variables significantly predicted the probability of nest predation (Table 2). Nest failure due to parasitism was low, as only three (6%) of the nests fledged only Brown-headed Cowbird young. Despite few total nest failures due to parasitism, the parasitism rate was high with 12 nests (25.5%) partially parasitized, although none of the independent variables significantly explained the pattern of nest parasitism (Table 2). Only seven of 47 nests (14.9%) escaped predation or parasitism.

DISCUSSION

Our results indicate that Red-eyed Vireos did not avoid forest edges for establishing ter-

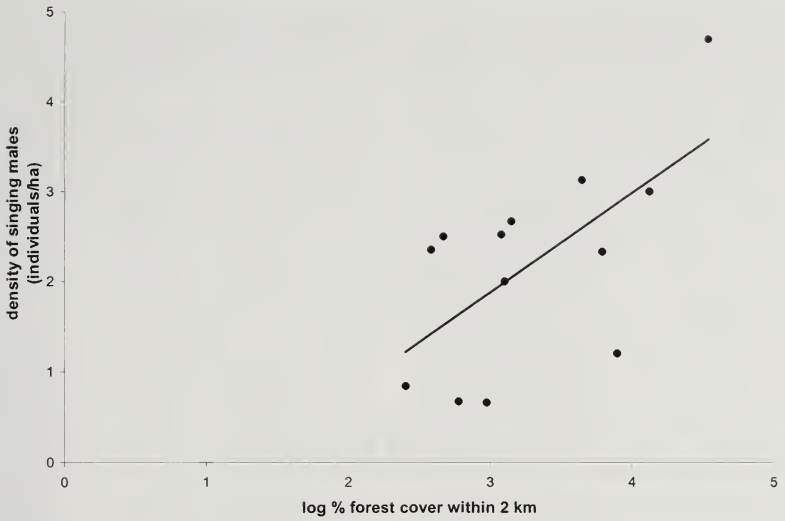

FIG. 3. Male Red-eyed Vireo density and the percent of forested habitat within a 2-km radius for 13 forest fragments in southcentral Ontario, Canada, during the 1996 and 1997 breeding seasons.

ritories or for nesting, and they were not an area sensitive species within our study region. Male density and pairing success increased only in relation to increasing forest cover within a 2-km radius of a study site, indicating that this species is not sensitive to fragment area but may be sensitive to the total amount of forest area within a relatively localized landscape context. However, the relationship between density and local forest cover appeared to be largely driven by one forest fragment with high local forest cover and high Red-eyed Vireo density (Fig. 3). Regardless of this uncertainty, these results help to clarify habitat associations of this species by offering evidence that they are neither edge avoiding nor area sensitive. This may explain why Red-eyed Vireos are one of the few Neotropical migrants to nest regularly in heavily wooded suburban areas and city parks (Peck and James 1987). Fragment occupancy by female and, perhaps less certainly, male Red-eyed Vireos appeared to be associated with the surrounding landscape context and not merely fragment area. This supports the findings of Villard et al. (1995) for some other Neotropical migrant bird species.

Our results, based on territory and nest locations as well as patterns of density and pairing success relative to forest edges, support the classification of the Red-eyed Vireo as an interior-edge generalist species rather than an edge avoiding species. The density of interior-edge generalists should not be related to fragment area, in contrast to forest interior species (Bender et al. 1998), as they are able to use edge habitat which comprises a greater proportion of small forest fragments. Although the mean distance to the forest edge from both territories and nests increased with fragment area, there was no evidence that Red-eyed Vireos actually were selecting interior territory or nest sites in preference to edge sites in larger fragments. The increased variability of territory and nest placement in larger forest fragments indicates that this species utilizes both edge and interior habitats even when large amounts of interior habitat are available, which supports the conclusion of plasticity in habitat requirements. Nesting habitat does not appear to be a limiting factor for Red-eyed

TABLE 1. Parameter estimates from multiple regression analysis of male Red-eyed Vireo density during the 1997 and 1998 breeding seasons in 13 forest fragments in southcentral Ontario, Canada.

Parameter	Slope	SE	*t*	*P*
Intercept	0.97	5.96	0.163	0.87
Fragment area	−0.16	0.176	0.91	0.38
Local forest cover	2.00	0.725	2.76	0.022
Regional forest cover	−1.04	0.822	1.33	0.22

TABLE 2. Parameter estimates from logistic regression analysis of four measures of Red-eyed Vireo reproductive success during the 1997 and 1998 breeding seasons in southcentral Ontario, Canada. *N* is the number of forest fragments studied.

Variable	*n*	Parameter	Coefficient	SE	χ^2	*P*
Pairing success	13					
		Intercept	−10.41	5.20	4.01	0.04
		Fragment area	−0.26	0.19	1.81	0.18
		Local forest cover	2.22	0.87	6.55	0.01
		Regional forest cover	−0.15	0.70	0.05	0.83
		Distance to the edge	0.17	0.27	0.82	0.54
Nesting success	8					
		Intercept	1.18	5.50	0.04	0.83
		Fragment area	−1.13	0.25	0.26	0.61
		Local forest cover	0.76	0.66	1.34	0.25
		Regional forest cover	−0.62	0.77	0.65	0.42
		Distance to the edge	0.084	0.24	0.11	0.72
Nest predation	8					
		Intercept	−7.71	5.65	1.86	0.17
		Fragment area	−0.23	0.28	0.71	0.39
		Local forest cover	−0.33	0.69	0.23	0.62
		Regional forest cover	1.11	0.78	2.01	0.15
		Distance to the edge	−0.10	0.24	0.18	0.67
Brood Parasitism	8					
		Intercept	3.71	6.04	0.38	0.54
		Fragment area	−0.53	0.41	1.67	0.19
		Local forest cover	0.09	0.77	0.01	0.89
		Regional forest cover	−0.35	0.88	0.16	0.67
		Distance to the edge	−0.69	0.31	1.04	0.30

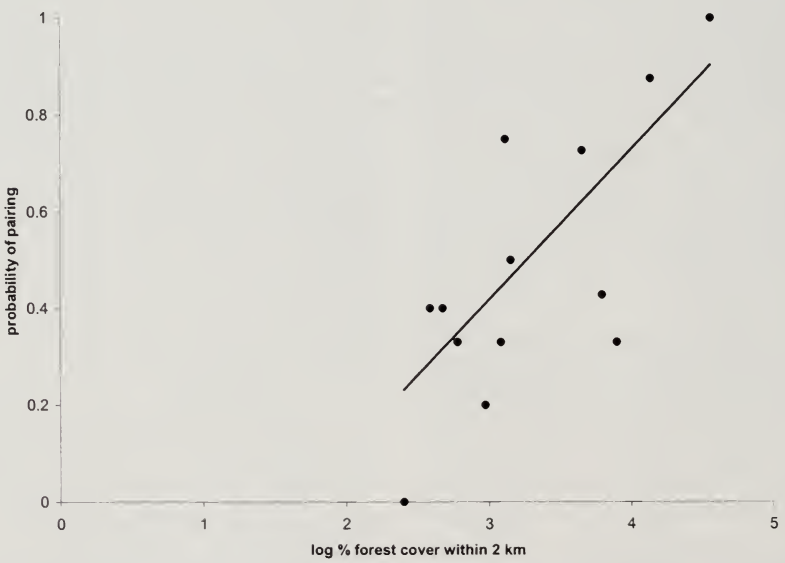

FIG. 4. Probability of a male Red-eyed Vireo pairing and the percent of forested habitat within a 2-km radius for 13 forest fragments in southcentral Ontario, Canada, during the 1996 and 1997 breeding seasons.

Vireos in small forest fragments within this part of southcentral Ontario.

In comparison to other forest bird species monitored within our study sites (Burke and Nol 2000), the rates of predation and parasitism on Red-eyed Vireo nests were high. The fate of Red-eyed Vireo nests did not vary with fragment area, forest cover, or distance from the nest to the edge. Although these results are based on a small sample of forest fragments, they are consistent with research based on a larger sample size conducted in our study region (Burke and Nol 2000). Our estimate of nest success may have been lower than that of the entire population because we monitored only nests that were <4 m high. Red-eyed Vireos can nest in the subcanopy and canopy of hardwood forests (Peck and James 1987) and these nests may, in general, avoid predation, since shrub nests have been identified as the most vulnerable to predators (Sargent et al. 1998). Locating and monitoring these high nests may provide a more accurate measure of nest success for this species.

The detection of edge effects on forest bird nest predation rates is common in forest fragments embedded in agricultural landscapes (reviewed in Paton 1994, Andren 1995), such as southcentral Ontario. However, composition of the local predator community is important to understanding the spatial pattern of nest predation (Andren 1995), as some studies have found that predation on birds' nests by avian predators is higher at forest edges and in small forest fragments while predation by small mammals is higher in forest interiors and larger fragments (Nour et al. 1993, Haskell 1995). We did not identify nest predators in our study and in combining all predation events may have masked trends in distance to the edge, fragment size, or forest cover by different types of predators.

Estimates of pairing success and, less certainly, density seem to indicate that Red-eyed Vireos preferred forest fragments embedded in areas of high forest cover, even though there did not appear to be any fitness consequences (increased nest success) in this preference. It is possible that our sample size of nests did not have the power to detect such relationships.

Although currently not a species of conservation concern, Red-eyed Vireos appear to occur at lower density and be less successful in attracting mates within regions of low local forest cover. It is therefore possible that if deforestation continues, populations of this species could begin to decline. This result supports the findings of Trzcinski et al. (1999) that habitat loss (decrease in forest cover) may be the most important factor affecting the distribution of forest breeding birds. Maintaining localized regions with high forest cover (>30%) has been recommended on numerous occasions for the conservation of area sensitive forest birds (Robbins et al. 1989, Freemark and Collins 1992, Freemark et al. 1995); our results suggest high forest cover also may benefit species that do not appear to be area sensitive. Large forest fragments often are embedded in landscapes with high forest cover, thus preserving these landscapes also would benefit both interior nesting species and interior-edge generalists.

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HABITAT USE AND BEHAVIOR OF MIXED SPECIES LANDBIRD FLOCKS DURING FALL MIGRATION

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ABSTRACT.—Little research has examined the ecology of mixed species flocks of migrant and resident landbirds during migratory periods. We studied habitat use and behavior of mixed species insectivorous landbird flocks during fall migration in central Pennsylvania. From late August to early October, 1998 and 1999, 220 flocks were observed for 30-min periods in six forest habitat types: mature forest interior, mature forest edge, mature forest agricultural edge, mature suburban forest, pole stage forest, and shrub/sapling stage forest. Sixty species were recorded in flocks that contained 2–24 species each (mean = 9.25 ± 0.29 SE). Flocks contained 2–181 individuals (mean = 22.12 ± 1.18 SE). Flocks in the six habitats had 49–61% Nearctic-Neotropical migrant individuals, 5–15% temperate migrants, and 23–37% residents. Abundance and species richness of migratory guilds (Nearctic-Neotropical migrants, temperate migrants, and resident species) within flocks were highest in structurally heterogeneous habitats (especially forest edge habitat) and were lowest in homogeneous pole stage forest. Of nine migrant species whose abundance varied significantly among habitats, six had highest abundance in flocks in forest edge habitat: Blue-headed Vireo (*Vireo solitarius*), Red-eyed Vireo (*V. olivaceus*), Blue-gray Gnatcatcher (*Polioptila caerulea*), Chestnut-sided Warbler (*Dendroica pensylvanica*), Black-throated Green Warbler (*D. virens*), and Magnolia Warbler (*D. magnolia*). Resident parids (Black-capped Chickadee, *Poecile atricapillus*, and/or Tufted Titmouse, *Baeolophus bicolor*) occurred within 82% of flocks and were observed leading 68% of these flocks. Movement rate (m/min) of flocks varied among habitats with flocks in edge-dominated habitats (forest edge, forest agricultural edge, and suburban forest) tending to have slower movement rates than in pole stage forest and forest interior, suggesting that food availability may have been greater in edge-dominated habitats. Consistently high species richness and abundance of migrant guilds and individual species strongly suggests that structurally diverse forest edge habitats were selected and provided relatively high quality stopover habitat for landbirds during fall migration. *Received 19 December 2000, accepted 20 October 2001.*

Birds face numerous challenges while migrating between breeding and nonbreeding locations. Aside from high energetic costs during migration, migrants must adjust to poor weather and unfamiliar habitats, compete with other migrant and resident birds, and avoid predators (Moore et al. 1995). Selection of high quality habitat during migration should allow migrants to face such challenges and meet energy requirements more efficiently, thereby increasing their chances for a successful migration. For example, in the Rio Grande Valley of New Mexico, Wilson's Warblers (*Wilsonia pusilla*) occurring in high quality stopover habitat (native willows) had higher rates of fat deposition and shorter stopover periods than in low quality habitat (Yong et al. 1998). Despite the importance of stopover habitat for migrants, there is surprisingly little information on patterns of habitat use and habitat quality during migration in North America (see Petit 2000 for a review).

Because both Nearctic-Neotropical and temperate migrant landbirds regularly join resident species in mixed species flocks during migration (Morse 1989), assessing differences among habitats in migrant abundance, species richness, and behavior within these flocks should provide information on important stopover habitats for migrants. However, very few studies have examined ecology or species composition of flocks in migration (but see Keast 1980, Morse 1989). Previous studies during migration (irrespective of flocks) have demonstrated that migrants select among available habitats and their abundance often is positively correlated with resource availability (reviewed in Moore et al. 1995 and Petit 2000), including both insects (Hutto 1985, Blake and Hoppes 1986) and fruit (Martin 1985, Blake and Hoppes 1986, Suthers et al. 2000). Given the importance of food resources to migrating birds, these studies suggest that habitats in which migrants are most abundant

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typically should be high quality stopover habitats. Migrant species richness also may be an indicator of migrant habitat quality. For example, on Horn Island off the coast of Mississippi, species richness and abundance of spring migrants were highest in scrub/shrub habitat (Moore et al. 1990), which is thought to be the most suitable habitat for replenishing fat stores (Moore and Aborn 2000).

We propose that flock behavior (i.e., movement rate) could provide an indirect measure of relative food availability within habitats and complement data on abundance and species richness. Flock movement rates often are recorded in studies of mixed species flocks, but typically have not been related to habitats or habitat quality. Morse (1970) noted that mixed species flocks moved more rapidly through unfavorable habitats, though he provided no data on the subject. However, there are reasons to expect such a relationship. Foraging speed (number of movements/min) of individual birds increases where food availability is low because birds that forage faster search larger amounts of substrate and increase their prey encounter rate (Robinson and Holmes 1982). For example, Lovette and Holmes (1995) found that American Redstarts (*Setophaga ruticilla*) foraged faster in Jamaican wintering habitats, where food availability was relatively low, than in Nearctic breeding habitats. In addition, Hutto (1990) suggested that movement rate (distance moved/time) of individuals should be negatively related to food availability, perhaps due to area restricted searching following successful prey attacks. Because prey handling time should increase in habitats with high food availability, we further expect this to lower an individual's movement rate. Although movement rates of individuals may not be directly related to those of mixed species flocks, such a relationship seems likely and, thus, we propose that flocks will move more slowly in habitats of high food availability.

We used abundance, species richness, and behavior of mixed species foraging flocks as indicators of habitat quality within six forest habitat types in central Pennsylvania. These habitats varied in local habitat structure and landscape characteristics (forest, suburban, or agricultural landscape matrix) and represent habitats that are commonly encountered by migrating landbirds in eastern North America. Specifically, we compared abundance of migratory guilds and individual species, species richness and composition, and movement rates of mixed species flocks among habitats to identify important habitats for migrating landbirds in inland areas. We expected that relatively high quality habitat would be indicated by a combination of high abundance and species richness of migrants within flocks and lower flock movement rate.

STUDY AREA AND METHODS

Study area.—We studied mixed species landbird flocks from 21 August to 10 October, 1998–1999, within the Ridge and Valley Province of Centre and Huntingdon counties, Pennsylvania (40° 42′ N, 77° 55′ W). Study areas included Rothrock State Forest, State Game Lands 176, suburban forests in the State College area, and private land. We sampled mixed species flocks within six mixed hardwood forest habitat types (forest interior, forest edge, forest agricultural edge, suburban forest, pole stage forest, and shrub/sapling stage forest; described below) that varied in local habitat structure and/or landscape characteristics (forest, suburban, or agricultural landscape matrix). Additional description of the study area is given in Rodewald (2001).

Habitat types.—Four mature forest habitats (forest interior, forest edge, forest agricultural edge, and suburban forest) varied in their landscape characteristics, and typically were 80–100 years old, 20–30 m tall, with largely unbroken canopies. Small canopy gaps resulting from one to several tree falls or unimproved roads (10–15 m wide) were not considered edge habitats because the forest canopy remained largely intact. Mature forests were the most vertically heterogeneous habitats (i.e., with canopy, midstory, and understory layers). However, forest interior habitat often was less vertically heterogeneous than other mature forests because understory shrubs and saplings usually were sparser. Forest interior habitat was located within forest-dominated landscapes.

Forest edge habitat also was located within forest-dominated landscapes and occurred at edges between mature forest and large forest openings with regenerating shrubs and saplings, e.g., power line right-of-ways, open canopy roads (>20 m wide), and regenerating clearcuts. Forest edge habitat had dense understory foliage along the edge, and a gradual edge (typically 5–15 m wide) between mature forest and shrub/sapling stage habitat.

Forest agricultural edges were located within a forest-agricultural landscape matrix and characterized by an abrupt edge (≤5 m wide) between an agricultural crop and mature forest. Forest agricultural edges had distinctly lower amounts of understory vegetation associated with the edge than the forest edge habitat type.

Suburban forest habitats were 6- to 14-ha mature forest stands dispersed within lightly wooded suburban housing developments and had relatively large amounts of edge habitat due to their small size. Therefore, we considered suburban forests to be edge-dominated habitats, similar to forest edge and forest agricultural edge habitats.

Pole stage forest habitats were within forest-dominated landscapes and were even-aged stands approximately 30 years old, <15 m tall, and with trees 10–25 cm diameter (dbh). These forests had a dense canopy with little understory vegetation and thus were not vertically heterogeneous in habitat structure.

Shrub/sapling stage forest habitats (i.e., early successional forests) were regenerating forest cuts within forest-dominated landscapes. These habitats had shrubs and saplings mostly 2–4 m tall and <8 cm dbh, and occasional larger trees ≤15 m tall. Shrub/sapling stage habitats lacked the vegetation layering of mature forest habitats, but did have a highly variable canopy layer due to differing heights of shrubs, saplings, and trees.

Plant species composition of habitats.—Common to fairly common tree species of study habitats included white oak (*Quercus alba*), northern red oak (*Q. rubra*), chestnut oak (*Q. prinus*), red maple (*Acer rubrum*), sugar maple (*A. saccharum*), black gum (*Nyssa sylvatica*), black cherry (*Prunus serotina*), black birch (*Betula lenta*), and hickories (*Carya* spp.). Conifers such as eastern white pine (*Pinus strobus*), pitch pine (*P. rigida*), and eastern hemlock (*Tsuga canadensis*) were less common in the study area. Common to fairly common woody understory plants of forest interior, forest edge, and forest agricultural edge included saplings of canopy tree species (especially red maple), as well as blueberries (*Vaccinium* spp.), mountain laurel (*Kalmia latifolia*), and witch-hazel (*Hamamelis virginiana*). Non-native bush honeysuckles (*Lonicera* spp.), common privet (*Lingustrum vulgare*), and red maple saplings were most common in suburban forest understory.

Flock observations.—During fall, the patchy distribution of mixed species bird flocks and the lower detectability of less vocal migrants made traditional bird survey methods (e.g., point-counts, line-transects) less efficient for documenting migrant habitat use patterns. Thus, we recorded habitat use and behavioral data while following mixed species bird flocks. We defined mixed species flocks as an assemblage of two or more species occurring <25 m of each other and moving together during an observation period (Hutto 1987). We examined insectivore flocks that contained ≥1 migrant species and often moved widely during an observation period. We did not collect data on mixed species flocks of *Catharus* and *Hylocichla* thrushes and other species that are strongly frugivorous during fall (Parrish 1997, 2000); such flocks were more sedentary and focused their foraging effort within areas with fruiting plants. However, several species, including Red-eyed Vireo (*Vireo olivaceus*) and Rose-breasted Grosbeak (*Pheucticus ludovicianus*), occurred in both frugivore and insectivore flocks. Similarly, we did not examine mixed species flocks of granivorous species (e.g., sparrows).

We observed flocks from 06:00–16:00 EST, but 85% of flock observations were made prior to 12:00. We sampled flocks equally across habitats with respect to time of day. Flocks were located by walking through study habitats while listening for call notes of flock members and searching visually for birds. We followed flocks for up to 30 min when possible. After sampling a flock, we were careful not to resample the same flock and typically moved >250 m from the location before collecting additional data. Sampling of flocks was done over extensive areas and not at specific sites that were regularly revisited. On occasions when the same general area was resampled, several days had elapsed since the previous visit. Given this pattern of sampling, it seems very unlikely that we observed the same flock of individuals more than once on the same or different days.

We recorded species richness and abundance of species that attended mixed species flocks. When it was not possible to count each flock member during an observation period, we made a conservative estimate of the number of additional birds in the flock. At 2-min intervals, we visually estimated the distance from the center of the flock to the nearest habitat edge, and recorded flock activity (e.g., foraging, resting) and habitat type used. At the end of an observation, we estimated total distance traveled by the flock by pacing the path taken by the flock back to the starting point of the observation.

Nearly all flocks used a single habitat type during an observation period. On occasions when flocks used more than one habitat, they were categorized as using the habitat in which they spent the majority of the observation period. We considered flocks to be using forest interior habitat when their mean distance to a habitat edge was >50 m and the flock did not use edges during an observation period. We considered flocks to be using edge habitats (i.e., forest agricultural edge and forest edge) if their mean distance to the habitat edge was <50 m during an observation period.

We recorded whether parids (Black-capped Chickadee, *Poecile atricapillus*, and/or Tufted Titmouse, *Baeolophus bicolor*) led flocks. Parids were considered to lead flocks when an individual(s) flew from an area of flock foraging activity to a new area, and was promptly followed by flights of other flock species oriented in the same direction (Morse 1970). Because only unambiguous observations of leading were collected, our estimates of leading by parids represent minimum values (Morse 1970).

Statistical analysis.—We classified flocking species as Nearctic-Neotropical migrants following DeGraaf and Rappole (1995), with the exception that Blue-headed Vireo (*Vireo solitarius*), Golden-crowned Kinglet (*Regulus satrapa*), Ruby-crowned Kinglet (*R. calendula*), Yellow-rumped Warbler (*Dendroica coronata*), and Pine Warbler (*D. pinus*) were classified as temperate migrants because they winter mainly

north of 25° N (American Ornithologists' Union 1998, Poole and Gill 1993–2001); remaining species were classified as temperate migrants or residents (American Ornithologists' Union 1998; Table 1). For each flock observed, we calculated species richness for all species combined (i.e., total richness) and for each migratory guild. We calculated abundance for all species combined (i.e., total abundance), migratory guilds, and individual species. Using only flock observations lasting >15 min, we calculated mean movement rate and mean distance to nearest habitat edge for each flock.

We conducted statistical analyses using SAS software (SAS Institute, Inc. 1990). We checked data for normality and homogeneous variance, and variables that did not meet assumptions for parametric tests were log transformed. Statistically significant results were indicated at $P < 0.05$. In the absence of significant annual differences, we pooled flock data across years. For each migratory guild and for all species combined we examined differences in species richness and abundance among habitats using analysis of covariance (ANCOVA) with habitat type as the main factor and time of day as a covariate. We used this same analysis to test for differences among habitats in the abundance of individual species within flocks (only species with ≥15 observations were included). ANCOVA also was used to examine differences in flock movement rate among habitats, with covariates being total abundance within flock and time of day. Total abundance was included to control for the effect of flock size because this is positively related to flock movement rate (Morse 1973). Time of day was included as a covariate because there was a negative correlation between time of day and most measures of species richness, abundance, and flock movement rate. When we obtained a significant result in the above analyses, we made pairwise comparisons among habitats using ANOVA, and controlled experimentwise error at 0.05 using the Bonferroni method. We used correlation analysis to test for a relationship between distance to nearest habitat edge and time of day for flocks that occurred in the three edge-dominated habitats (forest edge, forest agricultural edge, and suburban forest).

RESULTS

We observed 220 flocks in the six habitat types during fall 1998 and 1999. Sample sizes for flocks in each habitat were forest interior (57), forest edge (41), forest agricultural edge (38), suburban forest (30), pole stage forest (21), and shrub/sapling stage forest (33). Flocks included nonbreeding transient species (e.g., Bay-breasted Warbler, *Dendroica castanea*), both transient and postbreeding individuals of migratory species that bred locally (e.g., Black-throated Green Warbler, *D. virens*), and resident species. Individuals within flocks occasionally were observed preening or resting, but spent the large majority of their time actively foraging. Flock members foraged primarily on arthropods during observation periods. Some individuals did consume fruit; however, flocks did not linger in fruiting trees or shrubs. Of migratory species we studied, few lone individuals were encountered outside flocks, suggesting a strong propensity to flock during fall stopover for these migrant landbirds.

We observed 167 flocks for ≥15 min. Within the three edge-dominated habitats (forest edge, forest agricultural edge, and suburban forest), there was a positive relationship ($r = 0.25$, $P = 0.017$, $n = 86$) between distance to nearest edge habitat and time of day, such that flocks foraged closer to edges during morning. In addition, flocks in edge-dominated habitats typically spent the entire observation period <10 m from the actual habitat edge.

Species richness within flocks.—We recorded 60 species attending mixed species insectivorous bird flocks, including 41 Nearctic-Neotropical migrant species, 13 temperate migrant species, and six resident species. Individual flocks contained 2–24 species with a mean of 9.25 (±0.29 SE) species. No significant interaction between habitat and year was detected for species richness of Nearctic-Neotropical migrants ($P = 0.74$), temperate migrants ($P = 0.56$), or resident species ($P = 0.59$), so richness data were pooled by year for each guild. Both total richness ($F_{5,213} = 11.51$, $P < 0.001$) and richness of Nearctic-Neotropical migrants ($F_{5,213} = 4.28$, $P = 0.001$) within flocks differed among habitats and were highest in forest edge and lowest in pole stage forest (Table 2); time of day was a significant covariate for both total richness ($P = 0.008$) and richness of Nearctic-Neotropical migrants ($P = 0.013$). Species richness of temperate migrants varied ($F_{5,213} = 4.04$, $P = 0.002$) among habitats and was highest in flocks in both forest interior and forest edge and lowest in pole stage forest (Table 2), but did not vary significantly with time of day ($P = 0.87$). Resident species richness differed ($F_{5,213} = 11.24$, $P < 0.001$) among habitats and was highest in forest edge and lowest in flocks in pole stage forest (Table 2), but did not vary significantly with time of day ($P = 0.17$).

Guild and total abundance within flocks.—Single flocks contained 2–181 individuals

with a mean of 22.12 (±1.18 SE) individuals. Individual flocks had 49–61% Nearctic-Neotropical migrants, 5–15% temperate migrants, and 23–37% residents. No significant interactions between habitat and year were detected for abundance of Nearctic-Neotropical migrants ($P = 0.83$), temperate migrants ($P = 0.20$), and residents ($P = 0.59$), so abundance data were pooled by year for each guild. Abundance of both Nearctic-Neotropical migrants ($F_{5,213} = 6.30$, $P < 0.001$) and all species combined (i.e., total abundance; $F_{5,213} = 12.66$, $P < 0.001$) differed among habitats and were highest in flocks in forest edge, whereas flocks in pole stage forest had only one quarter as many individuals; abundance of Nearctic-Neotropical migrants and all species combined were intermediate within flocks in remaining habitats (Table 2). Time of day was a significant ($F_{1,213} = 6.61$, $P = 0.011$) covariate and was negatively related to Nearctic-Neotropical migrant abundance. Abundance of temperate migrants within flocks differed ($F_{5,213} = 4.80$, $P < 0.001$) among habitats with highest numbers in forest interior and lowest numbers in pole stage forest (Table 2). Resident abundance within flocks differed ($F_{5,213} = 5.03$, $P < 0.001$) among habitats and was highest in forest edge and lowest in pole stage forests (Table 2).

Abundance of individual species within flocks.—Of 60 species that occurred within flocks, 33 had adequate sample sizes for statistical analysis, and abundance of 12 of these species varied significantly among habitats (Table 1). Of nine migrant species whose abundance varied among habitats, six had highest abundance in flocks in forest edge habitat (Blue-headed Vireo; Red-eyed Vireo; Blue-gray Gnatcatcher, *Polioptila caerulea*; Chestnut-sided Warbler, *Dendroica pensylvanica*; Black-throated Green Warbler; and Magnolia Warbler, *D. magnolia*), but not significantly different from that in 1–3 other habitats. Downy Woodpeckers (*Picoides pubescens*), White-breasted Nuthatches (*Sitta carolinensis*), and Tufted Titmice were most abundant in the four mature forest habitats. For the habitat types studied, 67% of the 33 species were recorded within flocks in all six habitats, 27% occurred in five habitats, and 6% occurred in only four habitats (Table 1). However, species were heavily skewed in their abundance and many of the 33 species occurred primarily within 3–4 habitats and were found only a few times (or not at all) in pole stage forest.

Many species that joined flocks were recorded in numbers too low to permit statistical analysis (see Appendix). Of species recorded infrequently within flocks, forest edge habitats had the most species with high mean abundance relative to other habitats, but many species also were abundant in flocks in shrub/sapling stage forest, forest interior, and forest agricultural edges.

Parids occurred in 82% of mixed species flocks and were observed leading at least 68% of these flocks. Abundance of parids within flocks did not differ significantly among habitats or in relation to time of day ($F_{5,213} = 1.68$, $P = 0.14$).

Flock movement rate.—Movement rate of flocks varied among habitats ($F_{5,159} = 2.77$, $P = 0.019$), but there were no significant pairwise differences after Bonferroni adjustment. However, flocks tended to move more rapidly in pole stage forest and forest interior habitats (Fig. 1) than in shrub/sapling stage and edge-dominated habitats (forest edge, forest agricultural edge, and suburban forest). Movement rate was positively associated ($F_{1,159} = 13.33$, $P < 0.001$) with total abundance of birds within flocks, but not with time of day ($F_{1,159} = 2.7$, $P = 0.10$).

DISCUSSION

Migrating insectivorous landbirds in mixed species flocks used structurally heterogeneous habitats more than homogeneous pole stage forests. Among heterogeneous habitats, three lines of evidence suggested that forest edges were selected and provided high quality stopover habitat for migrating landbirds. First, both flock size (i.e., total abundance) and abundances of many individual species were greatest in forest edges (e.g., power line right-of-ways, open canopy forest roads, edges of forest cuts). In addition, bird survey data (Rodewald 2001) collected along transects in these habitats during fall indicated that edge-dominated habitats had significantly more flocks than other habitats.

Second, species richness within flocks typically was higher in forest edges than in other habitat types. In contrast, pole stage forests

TABLE 1. Abundance per flock for individual species that occurred within mixed species landbird flocks in six habitats in the Ridge and Valley Province of central Pennsylvania, fall 1998 and 1999. Flock sample sizes are in parentheses.

	Forest interior (57)		Forest edge (41)		Forest agricultural edge (38)		Suburban forest (30)		Pole stage forest (21)		Shrub/sapling stage forest (33)		
Species and migratory guild[a]	Mean	SE[b]	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	ANCOVA *P*
Red-bellied Woodpecker (*Melanerpes carolinus*)[R]	0.03	0.02	0.20	0.11	0.18	0.08	0.20	0.07	0.00	0.00	0.00	0.00	0.087
Downy Woodpecker (*Picoides pubescens*)[R]	0.69	0.10^{A}	0.77	0.12^{A}	0.63	0.10^{AB}	0.57	0.13^{AB}	0.05	0.05^{B}	0.27	0.10^{B}	<0.001
Hairy Woodpecker (*P. villosus*)[R]	0.19	0.07	0.22	0.08	0.05	0.04	0.03	0.03	0.05	0.05	0.03	0.03	0.074
Eastern Wood-Pewee (*Contopus virens*)[N]	0.52	0.13	0.65	0.17	0.55	0.18	0.40	0.14	0.00	0.00	0.36	0.12	0.091
Blue-headed Vireo (*Vireo solitarius*)[T]	0.50	0.10^{AB}	0.72	0.17^{A}	0.13	0.06^{B}	0.33	0.15^{AB}	0.14	0.10^{B}	0.45	0.13^{AB}	0.009
Philadelphia Vireo (*V. philadelphicus*)[N]	0.12	0.05	0.15	0.09	0.08	0.04	0.07	0.05	0.05	0.05	0.12	0.07	0.853
Red-eyed Vireo (*V. olivaceus*)[N]	1.76	0.34^{AB}	2.52	0.56^{A}	1.95	0.35^{AB}	1.50	0.36^{AB}	0.62	0.22^{B}	0.61	0.17^{B}	0.003
Black-capped Chickadee (*Poecile atricapillus*)[R]	3.09	0.35	3.25	0.43	2.71	0.29	2.03	0.45	2.52	0.49	2.94	0.39	0.469
Tufted Titmouse (*Baeolophus bicolor*)[R]	0.72	0.17^{C}	1.62	0.24^{B}	1.79	0.26^{B}	2.77	0.37^{A}	0.48	0.26^{C}	0.82	0.27^{BC}	<0.001
White-breasted Nuthatch (*Sitta carolinensis*)[R]	1.05	0.12^{A}	1.05	0.16^{A}	0.89	0.14^{AB}	1.07	0.21^{A}	0.00	0.00^{C}	0.36	0.10^{BC}	<0.001
Brown Creeper (*Certhia americana*)[T]	0.26	0.08	0.12	0.10	0.05	0.04	0.17	0.08	0.05	0.05	0.00	0.00	0.155
Golden-crowned Kinglet (*Regulus satrapa*)[T]	0.67	0.26	0.52	0.22	0.03	0.03	0.20	0.17	0.19	0.15	0.21	0.14	0.255
Ruby-crowned Kinglet (*R. calendula*)[T]	1.15	0.35^{A}	0.75	0.26^{AB}	0.16	0.07^{B}	0.33	0.20^{AB}	0.38	0.20^{AB}	0.21	0.11^{AB}	0.022
Blue-gray Gnatcatcher (*Polioptila caerulea*)[N]	0.14	0.06^{AB}	0.35	0.12^{A}	0.05	0.04^{B}	0.10	0.06^{A}	0.00	0.00^{B}	0.06	0.06^{B}	0.012
Tennessee Warbler (*Vermivora peregrina*)[N]	0.21	0.06	0.22	0.12	0.13	0.07	0.07	0.05	0.09	0.07	0.21	0.10	0.833
Nashville Warbler (*V. ruficapilla*)[N]	0.17	0.06	0.35	0.13	0.39	0.10	0.13	0.06	0.19	0.09	0.36	0.12	0.311
Chestnut-sided Warbler (*Dendroica pensylvanica*)[N]	0.33	0.10^{B}	1.47	0.37^{A}	0.50	0.14^{B}	0.53	0.17^{B}	0.05	0.05^{B}	1.03	0.21^{AB}	<0.001
Magnolia Warbler (*D. magnolia*)[N]	0.65	0.12^{B}	2.27	0.51^{A}	1.24	0.28^{AB}	1.23	0.19^{AB}	0.71	0.17^{B}	1.33	0.22^{AB}	<0.001
Cape May Warbler (*D. tigrina*)[N]	0.26	0.10	0.35	0.13	0.39	0.14	0.03	0.03	0.14	0.08	0.61	0.18	0.097
Black-throated Blue Warbler (*D. caerulescens*)[N]	0.62	0.12	0.27	0.09	0.34	0.11	0.40	0.12	0.43	0.16	0.64	0.17	0.209

TABLE 1. CONTINUED

Species and migratory guild[a]	Forest interior (57)		Forest edge (41)		Forest agricultural edge (38)		Suburban forest (30)		Pole stage forest (21)		Shrub/sapling stage forest (33)		
	Mean	SE[b]	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	ANCOVA *P*
Yellow-rumped Warbler (*D. coronata*)[T]	1.15	0.57	0.62	0.35	0.18	0.12	0.13	0.10	0.00	0.00	1.21	0.78	0.075
Black-throated Green Warbler (*D. virens*)[N]	1.31	0.20[B]	2.17	0.30[A]	0.89	0.16[B]	0.63	0.17[B]	0.62	0.22[B]	1.00	0.22[B]	<0.001
Blackburnian Warbler (*D. fusca*)[N]	0.48	0.10	0.77	0.18	0.34	0.12	0.30	0.15	0.14	0.10	0.45	0.15	0.105
Pine Warbler (*D. pinus*)[T]	0.17	0.08[A]	0.40	0.14[A]	0.13	0.09[A]	0.03	0.03[A]	0.00	0.00[A]	0.61	0.22[A]	0.011
Bay-breasted Warbler (*D. castanea*)[N]	0.31	0.08	0.45	0.12	0.24	0.08	0.13	0.08	0.00	0.00	0.27	0.11	0.064
Blackpoll Warbler (*D. striata*)[N]	1.03	0.22	0.90	0.23	1.13	0.26	0.93	0.20	0.81	0.22	0.27	0.14	0.118
Black-and-white Warbler (*Mniotilta varia*)[N]	0.26	0.08	0.52	0.13	0.37	0.10	0.27	0.14	0.09	0.07	0.54	0.13	0.136
American Redstart (*Setophaga ruticilla*)[N]	0.28	0.09	0.62	0.16	0.53	0.18	0.43	0.14	0.09	0.09	0.73	0.18	0.095
Ovenbird (*Seiurus aurocapillus*)[N]	0.24	0.09	0.12	0.06	0.05	0.04	0.20	0.10	0.05	0.05	0.09	0.05	0.298
Wilson's Warbler (*Wilsonia pusilla*)[N]	0.00	0.00	0.15	0.09	0.08	0.06	0.03	0.03	0.00	0.00	0.15	0.08	0.210
Canada Warbler (*W. canadensis*)[N]	0.05	0.03	0.20	0.07	0.05	0.05	0.10	0.06	0.05	0.05	0.24	0.10	0.094
Scarlet Tanager (*Piranga olivacea*)[N]	0.41	0.10[A]	0.60	0.19[A]	0.68	0.20[A]	0.20	0.09[A]	0.00	0.00[A]	0.24	0.09[A]	0.032
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)[N]	0.15	0.08	0.22	0.18	0.24	0.12	0.07	0.05	0.00	0.00	0.09	0.05	0.524

[a] N = Nearctic-Neotropical migrant, T = temperate migrant, R = resident/nonmigrant.
[b] Column means with the same letter were not significantly different (pair-wise ANOVAs; experimentwise error rate controlled at $\alpha = 0.05$ using Bonferroni method).

TABLE 2. Species richness and abundance of migratory guilds within mixed species landbird flocks in six habitats in the Ridge and Valley Province of central Pennsylvania, fall 1998 and 1999. Flock sample sizes are in parentheses.

Variable	Forest interior (57)		Forest edge (41)		Forest agricultural edge (38)		Suburban forest (30)		Pole stage forest (21)		Shrub/sapling stage forest (33)		ANCOVA P
	Mean	SE[b]	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	
Nearctic-Neotropical migrant richness[a]	5.33	0.42^{AB}	7.46	0.64^{A}	6.60	0.58^{A}	4.97	0.41^{AB}	3.43	0.44^{B}	6.36	0.75^{AB}	0.001
Temperate migrant richness	1.44	0.22^{A}	1.37	0.20^{AB}	0.60	0.15^{B}	0.67	0.21^{AB}	0.43	0.20^{B}	1.18	0.20^{AB}	0.002
Resident richness	2.42	0.17^{A}	3.00	0.19^{A}	2.74	0.21^{A}	2.60	0.29^{A}	0.86	0.16^{B}	1.61	0.21^{B}	<0.001
Total richness	9.19	0.52^{B}	11.83	0.69^{A}	9.95	0.68^{AB}	8.23	0.57^{B}	4.71	0.44^{C}	9.15	0.89^{B}	<0.001
Nearctic-Neotropical migrant abundance	9.96	0.95^{AB}	18.51	3.85^{A}	11.63	1.54^{AB}	8.30	0.91^{ABC}	4.86	0.78^{C}	10.76	1.50^{BC}	<0.001
Temperate migrant abundance	4.33	1.04^{A}	3.27	0.67^{A}	0.79	0.19^{B}	1.23	0.45^{AB}	0.76	0.39^{B}	3.03	0.88^{AB}	<0.001
Resident abundance	5.70	0.53^{ABC}	7.19	0.56^{A}	6.26	0.50^{AB}	6.67	0.84^{AB}	3.09	0.63^{C}	4.42	0.63^{BC}	<0.001
Total abundance	23.03	1.90^{B}	33.63	4.46^{A}	20.60	1.73^{B}	17.43	1.64^{B}	8.95	1.04^{C}	20.64	2.38^{B}	<0.001

[a] Richness = total number of species in each migratory guild; Abundance = total number of individuals in each migratory guild.
[b] Habitat means with the same letter were not different (pair-wise ANOVAs; experiment-wise error rate controlled at $\alpha = 0.05$ using Bonferroni method).

consistently had the smallest and least diverse flocks.

Third, flock behavior suggested that food availability may have been higher in edge-dominated habitats than in other habitats. After accounting for variation in flock size, movement rates did vary among habitats, with flocks in edge-dominated habitats having low mean movement rates relative to flocks in pole stage forest and forest interior. While this suggests that food availability was greater in edge habitats, there were no pairwise differences ($P < 0.003$) among habitats after Bonferroni adjustment and sample size for flock movement rate was low in pole stage forests. Despite this, there is reason to expect that flocks in edge habitats would experience higher food availability because arthropods often are more abundant at forest edges than in forest interior (Helle and Muona 1985, Bedford and Usher 1994, Jokimäki et al. 1998).

Forest edges may have had high abundance and diversity of migrants simply because birds accumulate at edges. Studies of Black-capped Chickadee flocks during winter have reported that forest edges are used more frequently than forest interior because edges act as conduits and channel flock movement (Desrochers and Fortin 2000). Indeed, in our study flocks in edge-dominated habitats often remained close to edges throughout observation periods. However, these flocks often moved only short distances and had low movement rates relative to most interior habitats (pole stage and forest interior), and not the higher movement rates that would be expected if edges functioned primarily as channels of flock movement. In addition, high arthropod abundance at forest edges would be an important incentive for flock members to actively forage at edges. While the possibility exists that forest edges functioned, in part, as conduits to flock movement in our study, our observations suggest this was less important in explaining habitat use patterns of mixed species flocks during fall.

Several features of edge habitats may have contributed to their high use by migrants. In addition to higher invertebrate abundance, forest edges often have greater stem densities and structural diversity (Gysel 1951), higher fruit abundance (Blake and Hoppes 1986, Rodewald 2001), and presence of tall herbaceous

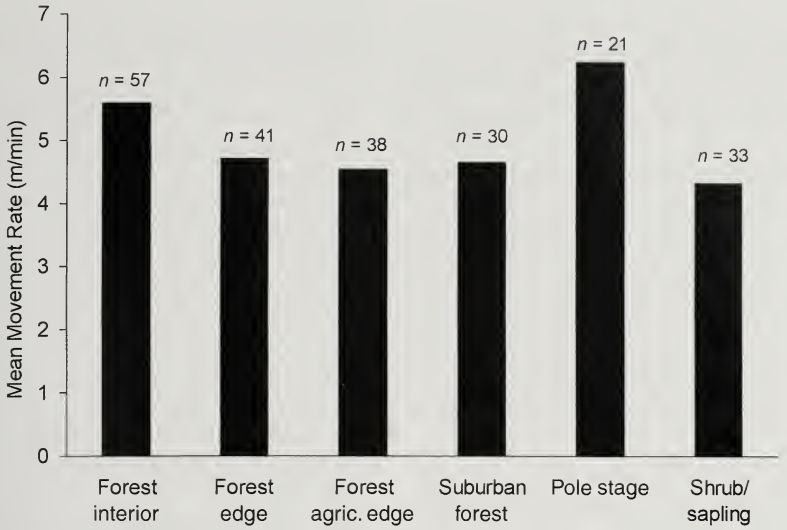

FIG. 1. Mean movement rate of mixed species landbird flocks in six forest habitats in the Ridge and Valley Province of central Pennsylvania during fall 1998 and 1999. Column means were not statistically different ($P > 0.003$) in pairwise comparisons (Bonferroni adjusted).

vegetation during late summer and fall. We observed that patterns of migrant abundance and richness seemed to be positively associated with habitat heterogeneity at edges. For example, pole stage forests, where there was little midstory and understory vegetation, had consistently low species richness and abundance of birds within mixed species flocks; pole stage forests have similar patterns of avian species richness and abundance during the breeding season (Conner and Adkisson 1975, DeGraff and Chadwick 1987). Also, forest agricultural edge habitat usually had notably lower density of shrubs and saplings compared to forest edge habitat, and this could explain differences in migrant abundance and richness between these two habitats. While little research has specifically examined habitat use by mixed species flocks during migration, several studies have reported relationships between habitat characteristics and migrant abundance and species richness. For example, heterogeneous vegetation of scrub/shrub and pine forest habitats on Gulf coast islands of Mississippi had higher abundance and species richness of spring migrants than less heterogeneous vegetation in primary dune and marsh/meadow habitats (Moore et al. 1990). In addition, foliage density was positively correlated with abundance of spring and fall migrant songbirds within forest tree fall gaps (Blake and Hoppes 1986, Martin and Karr 1986), and may provide denser protective cover, allowing migrants to lower their predation risk (Morse 1973, Grubb and Greenwald 1982).

Frugivory is frequent in many species of Nearctic-Neotropical migrant landbirds during migration (Parrish 2000). While some studies have suggested that fruit plays a minor role in lipid deposition in migratory birds (Berthold 1976, Izhaki and Safriel 1989), recent evidence suggests that fruit is far more important in promoting lipogenesis in some migrant species (Bairlein 1990, Parrish 1997). We observed individuals of a number of species that followed mixed species flocks consuming fruit, but flock members were largely insectivorous and flocks tended not to linger in fruiting plants. However, exceptions occurred when some species (e.g., Red-eyed Vireo and Rose-breasted Grosbeak) joined flocks of frugivorous birds (e.g., Cedar Waxwing, *Bombycilla cedrorum*, and American Robin, *Turdus migratorius*) and, in that situation, consumed fruit more readily. Overall, though, we do not believe that fruit resources at habitat edges were of primary importance in the selection of habitats by mixed species flocks we examined.

We regularly observed mixed species flocks of migrants foraging in areas with tall, dense herbaceous vegetation, such as mixed goldenrods (*Solidago* spp.), asters (*Aster* spp.), grasses (Poaceae), and corn (*Zea*). This vegetation occurred frequently within forest edge, forest agricultural edge, and shrub/sapling stage habitats during fall. Use of herbaceous nonfruiting vegetation by fall Nearctic-Neotropical migrants has been only anecdotally reported from eastern North America, but this behavior is not unusual during fall migration, especially for certain species of wood warblers (Dunn and Garrett 1997; PGR and MCB unpubl. data).

Mixed species flocks may have been attracted to edges for other reasons. Flocks that occurred in edge-dominated habitats during fall foraged closest to edges earlier in the day. This suggests that attraction to forest edges during morning may have been partly related to warmer temperatures at edges exposed to sunlight (Huertas and Diaz 2001) or higher light levels at edges than in adjacent forest. However, we regularly observed flocks during the afternoon within edge-dominated habitats when edges were not exposed to sunlight and on days with overcast skies.

The presence of parids in flocks may have attracted migrating birds as well. Moore and Aborn (2000) suggested that individual migrants may use parids and/or mixed species flocks as a selection cue for high quality habitat with higher resource availability. Joining flocks that contain residents during *en route* periods may be especially important for migrant landbirds because they typically are unfamiliar with local habitat and resource availability, having often arrived at a new stopover location during the previous night. Sampling habitats requires time, and migration is a time-limited period for migrants (Alerstam and Lindström 1990). Migrants that join flocks may benefit by increasing their foraging efficiency (Krebs et al. 1972) and lowering their risk of predation (Hamilton 1971, Morse 1980). Parids were present in over 80% of mixed species flocks and frequently were observed leading these flocks to new areas. Coupled with the fact that relatively few individuals of species that joined mixed species flocks were encountered outside flocks, it seems possible that parid occurrence influenced the habitat use of migrants.

Forest edges and structurally heterogeneous habitats seem to provide high quality fall habitat for many migratory landbirds during a critical period in their annual life cycles. While forest edge habitats are not considered high quality nesting habitat for many species of forest landbirds due to negative edge effects (Chasko and Gates 1982, Askins et al. 1987), they do seem to provide important resources for many species during migration. In addition, habitats with dense vegetation, including forest edges, have been shown to be important postbreeding (premigration) habitat for forest-breeding juvenile (Vega Rivera et al. 1998) and adult (Vega Rivera et al. 1999) Wood Thrushes (*Hylocichla mustelina*). Thus, effort should be made to improve and/or maintain existing edge habitat in certain local situations. Permanent and temporary anthropogenic edge habitats associated with suburban and agricultural woodlots, treerows in agricultural fields, forest cutting operations, power line right-of-ways, rural roads, and highways are examples of locations where land managers or private landowners could manage for heterogeneous habitat. However, because breeding season habitat requirements of migratory birds also must be considered, conservation benefits of local actions can be maximized only if developed within a regional context (Petit 2000). For example, maintenance or creation of edges to provide habitat for migrating landbirds may be inappropriate in large, contiguous forests given potential negative effects of edges on breeding landbirds. Ultimately, a better understanding of *en route* habitat relationships of migratory landbirds is needed to develop comprehensive conservation plans for these birds.

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APPENDIX. Landbird species that infrequently attended mixed species flocks in the Ridge and Valley Province of central Pennsylvania, fall 1998 and 1999. Sample sizes were insufficient to permit statistical analyses.

Yellow-billed Cuckoo (*Coccyzus americanus*)
Yellow-bellied Flycatcher (*Empidonax flaviventris*)
Least Flycatcher (*E. minimus*)
Great Crested Flycatcher (*Myiarchus crinitus*)
Eastern Phoebe (*Sayornis phoebe*)
Yellow-throated Vireo (*Vireo flavifrons*)
Warbling Vireo (*V. gilvus*)
Red-breasted Nuthatch (*Sitta canadensis*)
Winter Wren (*Troglodytes troglodytes*)
Northern Parula (*Parula americana*)
Blue-winged Warbler (*Vermivora pinus*)
Golden-winged Warbler (*V. chrysoptera*)
Orange-crowned Warbler (*V. celata*)
Yellow Warbler (*Dendroica petechia*)
Yellow-throated Warbler (*D. dominica*)
Prairie Warbler (*D. discolor*)
Palm Warbler (*D. palmarum*)
Cerulean Warbler (*D. cerulea*)
Worm-eating Warbler (*Helmitheros vermivorus*)
Connecticut Warbler (*Oporornis agilis*)
Mourning Warbler (*O. philadelphia*)
Hooded Warbler (*Wilsonia citrina*)
Common Yellowthroat (*Geothlypis trichas*)
Chipping Sparrow (*Spizella passerina*)
Dark-eyed Junco (*Junco hyemalis*)
Baltimore Oriole (*Icterus galbula*)

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SITE FIDELITY AND EPHEMERAL HABITAT OCCUPANCY: NORTHERN WATERTHRUSH USE OF PUERTO RICAN BLACK MANGROVES DURING THE NONBREEDING SEASON

LEONARD REITSMA,[1,2,6] PAMELA HUNT,[1,3] SHERMAN L. BURSON, III,[1,4] AND BENJAMIN B. STEELE[1,5]

ABSTRACT.—We studied the dispersion of Northern Waterthrushes (*Seiurus novaboracensis*) in southwestern Puerto Rico during four nonbreeding seasons, 1996–1999. Densities were high (up to 13 birds/ha) on a 3-ha mature black mangrove (*Avicennia germinans*) study plot, but were significantly lower during periods of high water levels. Individuals exhibited site fidelity within and between seasons. Feeding areas were small (mean = 0.074 ha ± 0.041 SD) and there was considerable overlap tolerated among conspecifics. Waterthrush density decreased when water submerged their primary foraging substrate: woody debris and pneumatophores. Interannual returns were similar to other Neotropical migrants (mean = 50%) but site persistence was low due to periodic flooding. In September 1998, hurricane Georges flooded the plot and blew down >90% of the black mangrove trees. This drastic habitat alteration was followed by a drastic decline in waterthrushes using the study area. Individuals left feeding areas for overnight roost sites in red mangroves (*Rhizophora mangle*). This latter finding, coupled with site fidelity and high return rates concurrent with low site persistence, suggests that waterthrushes exhibit high plasticity in their use of habitat during the nonbreeding season, but may rely upon mangroves for overwinter survival. *Received 15 May 2001, accepted 13 March 2002.*

Nearctic-Neotropical migratory passerines spend over half of each year in the tropics, commonly returning to the same sites (Faaborg and Arendt 1984, Lynch et al. 1985, Kricher and Davis 1986, Holmes et al. 1989, Winker et al. 1990). This realization has likely influenced the increase in studies that focus on winter habitat loss and its effect on populations of migrants. While almost all migrants are territorial during the breeding season, winter habitat use varies widely between species and many species' use of habitat is still poorly understood. Population studies recently have demonstrated that optimal nonbreeding habitat may be limiting, at least for some species (Rappole et al. 1989, Marra et al. 1998), thus the high rate of deforestation in Middle America and the Caribbean potentially will have a great impact on migrant bird populations (Rappole and Powell 1986, Wunderle and Waide 1994). Already, forest cover is estimated to have declined to about 21% of island land area in the Caribbean (Wunderle and Waide 1994).

Mangrove forests have some of the highest abundances of overwintering migrants in the Caribbean (Arendt 1992, Lefebvre et al. 1992, Robbins et al. 1992, Sliwa and Sherry 1992, Wunderle and Waide 1993). However, few detailed population studies have been conducted in mangroves (but see Holmes and Sherry 1992; Lefebvre et al. 1992, 1994; Lefebvre and Poulin 1996; Marra and Holmes 2001). Several studies have used marked individuals on the wintering grounds to quantify overwinter site persistence, annual return rates, and dispersion (Winker et al. 1990, Holmes and Sherry 1992, Mabey and Morton 1992, Staicer 1992, Wunderle 1992, Marra et al. 1998). Some migrants in mangroves defend territories (Holmes et al. 1989, Rappole et al. 1989, Mabey and Morton 1992).

The Northern Waterthrush (*Seiurus novaboracensis*) has been documented as the most abundant migrant passerine in some mangroves (Lefebvre et al. 1992, Wunderle and Waide 1993). Lefebrve et al. (1994) and Lefebvre and Poulin (1996) concluded this species was not territorial in either Venezuelan or Panamanian mangroves, respectively, in contrast to Schwartz's (1964) reports of territori-

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ality in this species within an irrigated botanical garden in Venezuela.

We monitored the use of a mature black mangrove (*Avicennia germinans*) forest by a marked population of Northern Waterthrushes over four nonbreeding seasons to determine whether this species (1) exhibits site fidelity in this habitat, and (2) responds to changes in habitat suitability within and between seasons. Natural changes that occurred during our study allowed us to document the degree of plasticity that this species exhibits in response to both short term and long term habitat changes.

STUDY AREA AND METHODS

We mapped the spacing pattern, and measured density and site persistence of Northern Waterthrushes on a 3-ha plot within a mature black mangrove forest. This site (18° 01′ N, 67° 10′ W) was located on the Boqueron Bird Refuge, a 182-ha reserve located 8 km south of Cabo Rojo in southwestern Puerto Rico and managed by the Puerto Rican Dept. of Natural Resources. This forest was separated from a red mangrove (*Rizophora mangle*) stand and open lagoons by a manmade dike. The plot had a mean canopy height of 12 m and a mean of 256 trees/ha, nearly all of which were black mangroves. The forest floor was a combination of shallow water (<25% cover when not flooded), leaf litter, mangrove pneumatophores, and woody debris. Waterthrushes foraged predominantly on the forest floor, but also searched for food on woody debris, upturned root masses, and in black mangrove trees.

Periodic flooding of the plot occurred throughout our study as a result of variations in rainfall between September and December. We measured water depth beginning in January 1997 using a gauge placed in a channel adjacent to the plot and calibrated the channel depth to the plot water depth. For time periods prior to the placement of the gauge in the field, we estimated the water levels by comparing the relative exposure of pneumatophores and percent open water cover on the plot. March 1997 and 1998 and January 1998 were similar in water level to the conditions prior to installing the gauge, and measurements during these three intervals allowed reasonably accurate estimates of the two periods previous to installation. Before Hurricane Georges, the mangrove forest had a closed canopy and little foliage below 2.5 m. The hurricane dramatically altered this habitat in September 1998, leaving <10% of the trees standing. The plot was still flooded 6 months after the hurricane, and little vegetative regrowth had occurred. We estimated the water levels for the periods after the hurricane by comparing the height of water on prominent standing trees and other unaltered features on and around the plot to flooded periods when the gauge was in place, such as January and October 1997.

We collected data in January during the 1995–1996 nonbreeding season (September through early April), and in October, January, and March for the following 3 years. We captured Northern Waterthrushes in mist nets, and color banded each bird. We measured weight, fat (0–4 visual index of interfurcular fat), and unflattened wing chord. During the last 2 years, we collected 5 μl of blood from the brachial vein of birds to sex individuals of this monochromatic species. We used a combination of PCR and electophoretic detection of diagnostic protein bands to determine sex (Griffiths et al. 1996) for some individuals, and nonoverlapping wing chord length distinctions in others (>78 mm for males, <71 mm for females; Pyle et al. 1987).

We systematically searched the plot for Northern Waterthrushes during each time period, and locations and movements of banded and unbanded birds were recorded. A bird was considered a resident if it was relocated ≥4 days in the same area in one time period of a single season. All observations were compiled during each trip to produce minimum activity ranges, which were the minimum convex polygons encompassing all observations of individual birds (Holmes et al. 1989). We refer to these minimum activity ranges as feeding areas rather than territories because individuals did not aggressively exclude conspecifics, but they did exhibit within and between season site fidelity, and they actively fed in these restricted areas. Interannual return rates and site persistence were based upon resightings and recaptures. We investigated movement of birds toward and away from the plot using mist netting during all three times of the nonbreeding season. An 80–120 m mist net lane was operated for 4 h after dawn and 4 h preceding dusk on the dike along the west edge of the plot. Travel direction was recorded for each bird captured.

We used simple regression to correlate water depth on the plot with bird density, and to correlate density with the amount of overlap in feeding areas. Overlap was quantified as the percent cover of the plot in which two or more feeding areas overlapped. We used chi square analysis to test for differences in travel direction of birds into the mist net lane after dawn compared to before dusk. Seasonal changes in body mass/wing chord ratios were analyzed using ANOVA to measure weight loss during the nonbreeding season. To obtain an adequate sample size for analysis of all three time periods of each season, the sample included all Northern Waterthrushes caught on the plot and on the dike adjacent to the plot, most of which did not have feeding areas on the plot. We also used a *t*-test to analyze differences in body mass/wing chord ratios for resident birds on the plot during October and January, for which we had adequate sample sizes.

RESULTS

The number of Northern Waterthrushes on the 3-ha study plot ranged from 39 in October 1996 to 0 in March 1999 (Fig. 1). Feeding areas were small (mean = 0.074 ha ± 0.041

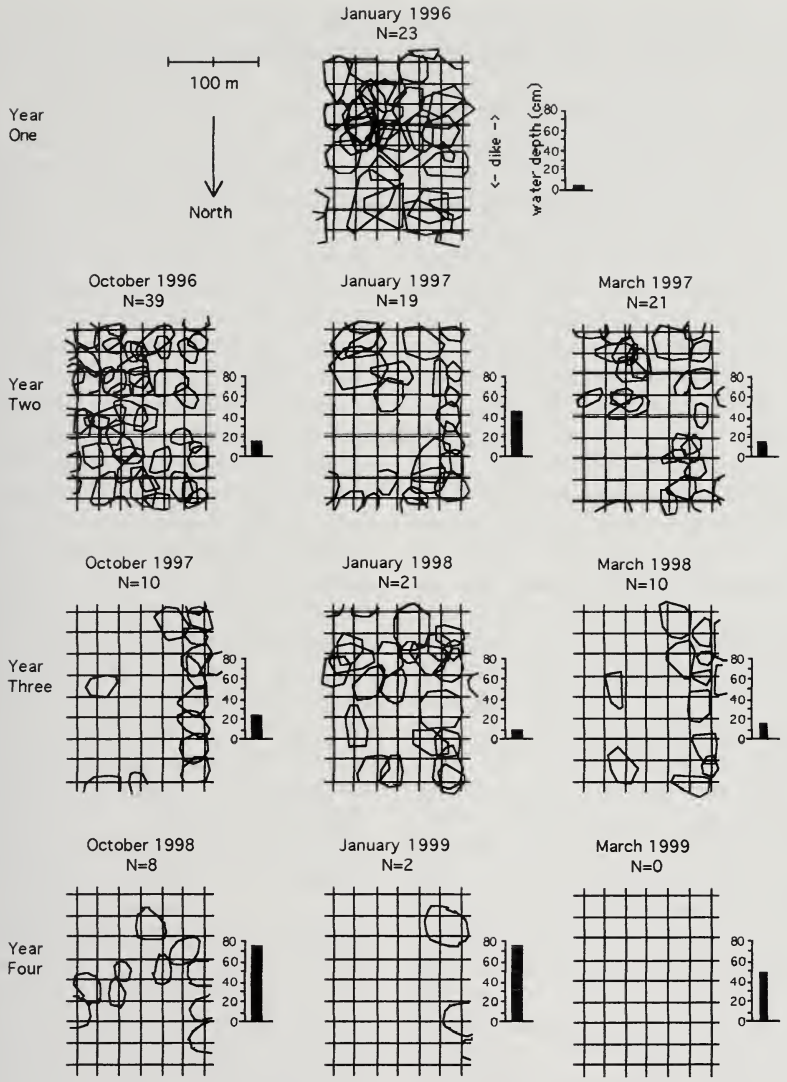

FIG. 1. Feeding areas of Northern Waterthrushes on a 3-ha mature black mangrove study plot at the Boqueron Bird Refuge in southwestern Puerto Rico during four nonbreeding seasons. Each polygon encloses all the observations of individually color-marked birds that were resighted ≥4 times on the plot during each designated time period. The number of mapped birds and the mean water depth of the plot (WD, in cm) is shown. The entire plot is covered with water when WD > 25 cm. The west side of the plot is bounded by a dike. Hurricane Georges drastically altered the structure of this forest plot in September 1998 just prior to Year Four. By March 1999, no resident birds remained.

SD, $n = 158$). During times of high density, there was greater overlap in feeding areas ($F_{1,8} = 26.49$, $P = 0.0009$, $r^2 = 0.768$). Density fluctuated widely within and between seasons and was negatively correlated with water depth ($F_{1,7} = 5.403$, $P = 0.049$, $r^2 = 0.403$). Flooding occurred between October 1996 and January 1997 with a corresponding >50% decline in density (Fig. 1). Flooding also occurred prior to October 1997 and October 1998 and was associated with much lower densities compared to October 1996. The lowest densities occurred after severe hurricane damage (October, January, and March of the

fourth season). Overall site persistence was low (42%) and varied from one interval to another.

Of 23 Northern Waterthrushes with well-documented feeding areas on the plot during January of 1996, 12 (52%) returned the following season and five (22%) returned again the next season. Return rates were lower between the second and third seasons of this study (8 of 26 birds, 31%) and lower still between the third and fourth seasons (2 of 14 birds, 14%). Of 63 well-mapped birds over the 4-year study, 21 (33% of the original cohort) had feeding areas in ≥2 consecutive years and five (7.9% of the original cohort) had feeding areas in three consecutive years. One of the 3-year occupants was recaptured the fourth season but did not have a known feeding area on the plot.

Waterthrushes lost mass throughout the season. The body mass/wing chord ratio of all waterthrushes, including transients, decreased throughout the nonbreeding season from October (mean = 0.23 g/mm ± 0.02 SD, n = 158) to January (0.22 ± 0.01 SD, n = 102) and then further in March (0.21 ± 0.02 SD, n = 9; $F_{2,226}$ = 4.71, P = 0.01). For resident birds, we had adequate sample sizes to compare only October to January, and the pattern was consistent (October mean = 0.23 ± 0.02 SD, n = 23, and January mean = 0.22 ± 0.02 SD, n = 47; t = 1.998, df = 68, P = 0.05).

Birds consistently moved across the dike from the red mangrove side in the morning and from the black mangrove side at dusk (n = 100, χ^2 = 37.37, df = 1, $P < 0.001$). Of the birds captured in the morning, 64% (n = 45) were going from red to black mangrove. Of the birds captured in the evening, 89% (n = 55) were going from black to red mangrove.

We determined the sex of 25 resident birds, 10 using blood DNA and 15 using wing chord lengths. Genetic analysis of blood showed no sex bias (6 of 10 sexed were males). The majority (14 of 15, 93%) of all birds sexed by wing chord length were females. Therefore, 7 of 25 birds of known gender with well-mapped feeding areas on the plot were male (28%). The sample sizes were too small to compare sex ratios within or between seasons. An additional 45 transients caught on or adjacent to the plot were sexed using blood DNA and 13 were males (28.9%), a proportion consistent with that of the residents.

DISCUSSION

When not flooded, this mature black mangrove forest had among the highest density (13 birds/ha) of marked resident birds of any previously recorded Neotropical migrant population (but see Marra and Holmes 2001, who reported 15 American Redstarts, *Setophaga ruticilla*, per ha during fall and 12/ha during spring). However, the conditions of this and other habitats (PH unpubl. data) used by Northern Waterthrushes were not stable. On the black mangrove plot, densities were inversely associated with water level. A similar pattern was documented in other habitats in southwestern Puerto Rico (LR unpubl. data). Moist ground appears to be the most suitable feeding substrate for waterthrushes in black mangroves, but standing water that submerges pneumatophore tips precludes their ability to forage on the ground. Woody debris and dead trunks remain useable when pneumatophores are submerged, but the majority of waterthrushes we observed foraging were walking on the ground among the pneumatophores. The linear dispersion of individuals along the drier dike during periods of flooding (Fig. 1: October 1997 and March 1998) provides further evidence for the importance of water level. These individuals had moist ground substrate for foraging, allowing them to persist along the edge of the plot.

The response of Northern Waterthrushes to Hurricane Georges was marked. The hurricane covered the plot with an estimated mean of 0.75 m of water and destroyed most of the canopy trees. Even though many birds were caught in nets on the dike and on the plot within 3 weeks after the hurricane, these birds likely were spending most of their time off the plot because only 2 of 48 caught on or near the plot were resighted. Bird activity on the plot declined during the 2 weeks following the hurricane, October 6–22, 1998, and was markedly lower still in January and March 1999. This probably was due to a lack of preferred foraging substrate because of the flooding and the disappearance of the canopy, which provided shade (see Schwartz 1964 for proposed minimum habitat requirements).

The fact that abundance on the plot varied

so greatly during each winter (19 to 39, 10 to 21, and 0 to 8) demonstrates the ability, and perhaps the necessity of waterthrushes to shift their daytime feeding areas. Although most of these birds were found repeatedly on one small part of the plot while they were residents, they went elsewhere when water covered the foraging substrate and they presumably found suitable habitat elsewhere. Individuals banded during October sometimes were not present during January, but were seen on the plot in March, indicating that the disappearance of birds from the plot during high water did not represent mortality but movement to other areas. This is consistent with the lack of season-long residence by waterthrushes in Panamanian mangroves (Lefebrve and Poulin 1996). In Panama, waterthrushes appeared to be tracking food abundance, and the authors suggested that the movement they documented may represent a broader pattern of midwinter migration for at least some species of Neotropical migrants. The large number of transient birds captured on or near the plot and never resighted suggests that many individuals simply moved through the plot. Recent evidence from telemetry suggests that many "transients" move considerable distances through many habitat types en route from regular feeding areas to roost sites (LR unpubl. data).

Although many species of Neotropical migrants are territorial during the nonbreeding season (Lynch et al. 1985, Holmes et al. 1989, Rappole et al. 1989, Marra et al. 1998), Northern Waterthrushes are not when they occupy mangroves (see also Lefebvre et al. 1994 and Lefebvre and Poulin 1996). Two to five individual feeding areas often overlapped, and overlap increased significantly with increasing density on the plot. Two to three individuals occasionally were observed <2 m from each other, and when flushed they often would fly in the same direction. Some individuals did, however, exhibit site fidelity to feeding areas, returning to the same specific areas on the plot on successive days and in successive years. Return rates were highest from first to second year (52%), and the lower rates in subsequent years may have been influenced by the higher incidence of flooding from 1997 through 1998. Schwartz (1964) documented classic territorial behavior during the second half of the nonbreeding season among a local population of Northern Waterthrushes within an urban park in Venezuela, but this territorial defense may have been in response to artificial ground moisture supplied by irrigation. Although most wintering migrants are territorial or occur in mixed species flocks, species with overlapping home ranges have been reported elsewhere in Puerto Rico (Staicer 1992).

The consistent predictable movement of individuals from black to red mangrove for overnight roosting was further supported by a minimal amount of radio telemetry (LR unpubl. data). Individuals that fed in the black mangroves traveled to the red mangroves across the dike in the evening and then back to the black mangroves the next morning. This use of red mangroves was further corroborated by more detailed studies at a site 6 km to the south and a site on the east side of Puerto Rico (LR unpubl. data).

Body mass to wing chord ratios declined throughout the nonbreeding season from October to March. This analysis was consistent for resident birds and for residents and transients combined. The pattern is similar to that which occurred in American Redstarts in Jamaica (Marra et al. 1998) and Belize (S. Baird unpubl. data). Body condition might be expected to decline given the general drying trend in most of Puerto Rico, and especially in the southwest, from January to the end of March, which often reduces arthropod abundance.

Individuals of both sexes had feeding areas on the plot. Birds that moved through the plot and those that remained on it to feed both showed similar sex ratios of three females to one male. Despite the fact that the majority (70%) of captured birds were not sexed and therefore the complete demographic makeup of this population was not known, our data suggest that waterthrushes do not appear to sexually segregate by habitat, at least to the same degree as some other migrant warblers such as the American Redstart (Marra and Holmes 2001, Parrish and Sherry 1994). We conclude that both sexes were residents on the plot for the duration of our monitoring, but we do not know the precise sex ratio at any single interval of our study.

The high density of Northern Waterthrushes documented in black mangroves in this study

and others (e.g., Lefebvre et al. 1994) indicates the importance of this habitat to sustaining waterthrush populations during the nonbreeding season. This habitat is subject to considerable short term change, mostly due to changes in water levels, but also due to changes in food abundance (Lefebvre and Poulin 1996). This might particularly influence its suitability for a ground forager such as the Northern Waterthrush. As a result, Northern Waterthrushes must be capable of changing locations over the course of any single nonbreeding season, and other locations and habitats may be essential to their survival. Lefebvre and Poulin (1996) suggest that migrant dwellers of mangroves may regularly migrate into and out of habitat patches, tracking the phenology of arthropod food in each. In our study, the changes in habitat quality resulting from flooding also may eliminate the benefits of territorial behavior in favor of more opportunistic occupation of suitable feeding sites.

Despite the documented within season mobility of this species, the high densities in mangroves, the return to mangroves when this habitat becomes suitable, and the daily movement back into red mangroves to roost, all underscore the importance of mangrove habitats to Northern Waterthrushes. The rapid human destruction of mangroves has the potential to cause declines in the species' population.

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OPPORTUNISTIC POLYGYNY IN THE LOUISIANA WATERTHRUSH

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ABSTRACT.—We monitored the nesting biology of color-banded populations of the Louisiana Waterthrush (*Seiurus motacilla*) at up to 25 sites across Pennsylvania from 1996–2001. Opportunistic polygyny in this species was documented for the first time during our study. Four out of 283 paired males were polygynous; one male and female were involved in a polygynous trio during two successive years. Opportunistic polygyny may have occurred primarily as a result of female territory fidelity and a locally skewed sex ratio in two cases, but appeared to be actively pursued as a mating strategy in the case of the male who was bigamous during two successive years. His aggressive territorial behavior was consistent with that reported for polygynous birds having naturally and experimentally elevated plasma levels of testosterone. The rate of nestling provisioning by this male at a failed secondary nest was substantially lower compared to his successful primary nest and compared to mean provisioning rates for monogamous males. In addition to reduced male parental care, protraction of the renesting interval following nest failure was another possible component cost of polygyny observed for one of the mates of this male. In this instance, both costs were borne by the first mated female, who was relegated to secondary status after her initial nest was depredated. *Received 9 April 2001, accepted 31 January 2002.*

Polygyny has been reported to occur opportunistically or facultatively in more than 15% of North American passerines generally characterized as having a monogamous mating system (Ford 1983). Since Ford's (1983) review, which listed differing levels of polygyny in 13 parulines, polygyny has been documented in several more wood warblers, typically during the course of long term population studies involving large numbers of uniquely color-marked individuals followed over several nesting seasons: Black-throated Blue Warbler (*Dendroica caerulescens*; Petit et al. 1988), American Redstart (*Setophaga ruticilla*; Secunda and Sherry 1991), Hooded Warbler (*Wilsonia citrina*; Evans-Ogden and Stutchbury 1994), Worm-eating Warbler (*Helmitheros vermivorus*; Hanners and Patton 1998), and Kentucky Warbler (*Oporornis formosus*; McDonald 1998). Within the genus *Seiurus*, early studies of nesting Ovenbirds (*Seiurus aurocapillus*) and Northern Waterthrushes (*S. noveboracensis*) found circumstantial evidence that polygyny may occur rarely (Hann 1937, Eaton 1949), but similar studies of Louisiana Waterthrushes (*S. motacilla*) did not (Eaton 1958).

Here, we document the first known cases of polygyny in the Louisiana Waterthrush based on observations made during ongoing studies of the breeding biology of the species in Pennsylvania. We studied nestling provisioning rates at two nests of one of the bigamous males and compared these to provisioning at nests of monogamous males at the same study site.

STUDY AREA AND METHODS

We confirmed polygyny during a study investigating the Louisiana Waterthrush as a bioindicator of the ecological integrity of forested headwater streams across Pennsylvania. Our study sites were 2–3 km reaches of 25 forested headwater streams in the three major river drainages in western (12 sites), central (seven sites), and eastern (six sites) regions of the state. Depending on the site, waterthrush populations were studied for 3–6 consecutive years between 1996 and 2001. We observed polygyny at three sites: Laurel Run (Huntingdon Co.; 40° 41′ N, 77° 51′ W; elevation 300 m) and Garner Run (Huntingdon Co.; 40° 40′ N, 77° 57′ W, elevation 400 m) in central Pennsylvania; and Powdermill Run (40° 09′ N, 79° 16′ W, elevation 500 m) in western Pennsylvania. In the following case histories, observations are referenced spatially according to numbered flags that were set at 50-m intervals from

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the lower end of each study stream, Flag 0, to the upper end, Flag 40–60, depending on overall stream reach length.

Each year we uniquely color banded most of the adult and nestling birds on our study sites. We attempted to locate and observe the nesting attempts of all nesting pairs. Nests were checked at least every 3–4 days, and selected nests were under almost daily observation from blinds placed 10–20 m away as part of detailed studies of incubation and nestling provisioning behavior in the species (RSM unpubl. data). Clutch initiation date (first egg laid), if not directly observed, was back calculated from known or estimated hatching and/or fledging dates, assuming 14-day incubation (beginning with the last egg laid) and 10-day nestling periods. The former, based on our own observations, is 1–2 days longer than indicated in most literature (e.g., Eaton 1958, Robinson 1995).

We conducted a total of 18 0.5- to 4.0-h nest watches in order to compare nestling provisioning rates of one bigamous male (total of 12.5 h of observation at his primary nest, 17.5 h at his secondary nest) and compared this with data collected during 253 h of observation at 20 nests of monogamous pairs on the same stream.

RESULTS AND DISCUSSION

Polygyny occurred very rarely during our study, in about 1% (4/283) of paired males. In western Pennsylvania one male was polygynous during two successive years. In each of the four confirmed cases, we observed a color-banded male during the same season in association with the nesting attempts of two different females, either both uniquely color-banded, or one banded and the other not.

The first case occurred on Laurel Run during 1999. During 1998, female BG (blue over green) nested successfully with male WR (white over red) on a territory that extended from Flags 0–7. She had nested with a different male in this territory the year before. In 1999, WR returned to the same 350-m long territory. We observed him with an unbanded female on 26 April, and their nest containing four nestlings was found on 24 May at Flag 5; their four young fledged on 28 May. By back calculation, the first egg was laid in this nest on 2 May (Fig. 1). Then, on 16 June, WR was seen associating with female BG, his mate from 1998, whom we had not observed previously on Laurel Run during 1999. We found a nest containing five young near fledging on 25 June near Flag 0, or about 250 m downstream of WR's first nest. We estimate that WR and BG initiated their clutch within a day or two of when young fledged from WR's primary nest with the unbanded female (Fig. 1). Presumably, WR and BG associated with one another (e.g., pairing, nest searching, nest building) for at least several days prior, during the nestling stage of WR's nest with the unbanded female.

Female Louisiana Waterthrushes show high levels of territory fidelity, with up to 50% of returning females reoccupying their territory from the previous year, not infrequently reuniting with the same mate (RSM unpubl. data), and this may have contributed to this case of polygyny. In Blackpoll Warblers (*Dendroica striata*), females returning to formerly held territories already occupied by a mated male were hypothesized to have the costs of sharing a mate offset by advantages associated with early nest initiation and familiarity with the territory (Eliason 1986; see also Wheelwright et al. 1992). Female BG and the unbanded female nested within the same territory used by WR and BG during the previous year, and by BG and a different male the year before that. It is possible that BG's arrival in 1999 on the territory she used during at least two previous years may have occurred after WR had already paired with an earlier-arriving female. BG may have accepted secondary status rather than incur possible costs related to delaying her breeding further by dispersing in search of a territory with an unmated male (Slagsvold et al. 1988). Alternatively, BG may in fact have been the primary female in terms of settling date, with loss of an earlier nesting attempt effectively relegating her to secondary status in terms of nesting (see Powdermill Run case histories below).

On Garner Run we discovered the nest of an unbanded waterthrush pair containing half-grown nestlings about 450 m below Flag 0 on 22 May 2000. We banded the male (blue over blue; BB) and female (blue over red; BR) associated with this nest on 26 May. We estimated that the pair initiated nesting on 30 April (Fig. 1). On 23 June, we observed BB with an unbanded female at Flag 11, or >1,000 m upstream of his earlier nest. Shortly thereafter, we found the pair's nest, which contained four nestlings estimated 4–5 days old, and we observed BB and the unbanded female feeding these nestlings. When we returned on 26 June to band the nestlings and

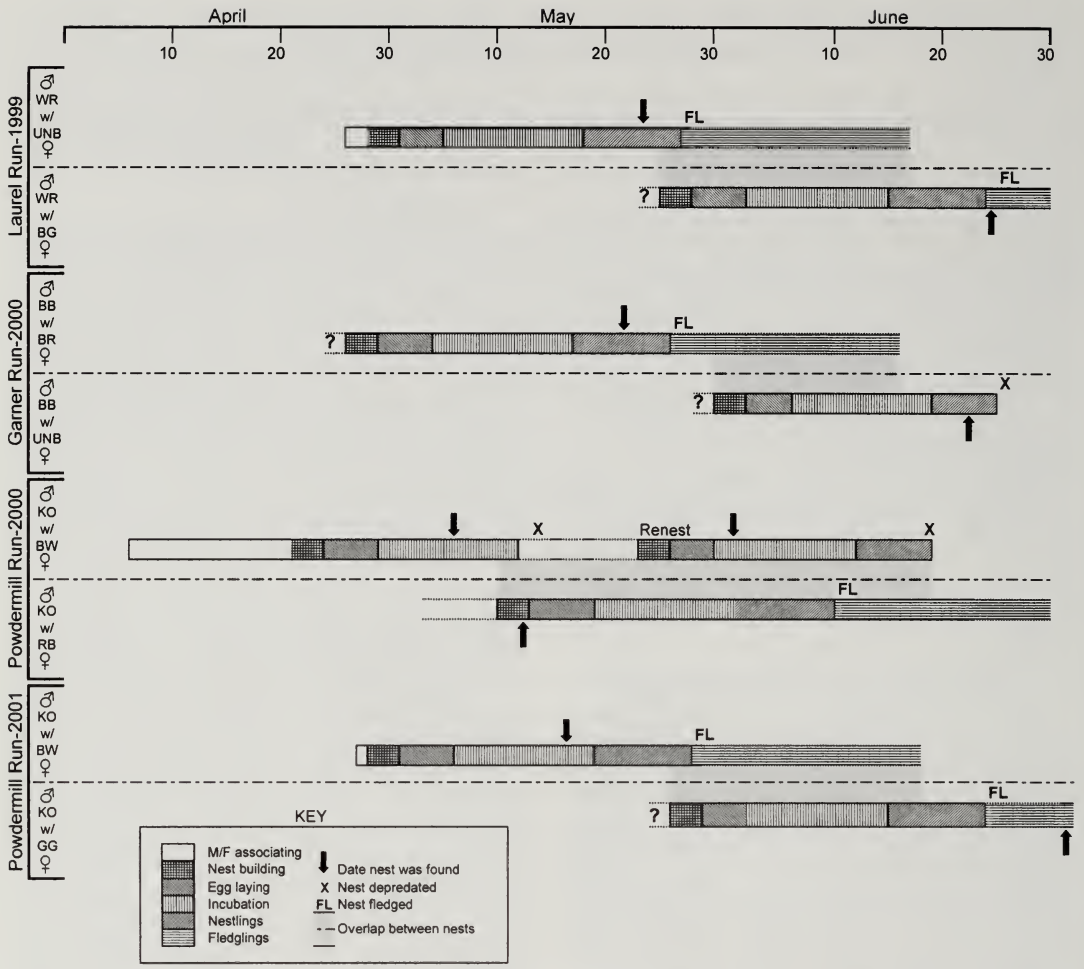

FIG. 1. Nesting chronologies of polygynous Louisiana Waterthrushes in Pennsylvania, 1999–2001. Transition dates for nesting stages prior to when nests were found were estimated based on back calculation from observed hatching or fledging dates (see Methods). Observed associations between members of a pair prior to the nest-building stage are bounded by solid lines, and inferred periods of associations have dashed lines. Question marks indicate cases where there was no observation of a pair prior to discovery of their nest. Similarly, solid lines indicate dates when fledgling care was directly observed; dashed lines when it was inferred. For nesting overlaps we assumed a 3-day nest-building period and maximum 3-week postfledging period.

the female, we found that the nest had been depredated. Based on the estimated age of the nestlings when the nest was found, the nest was initiated on 3 June, or about a week after the BB's first brood had fledged. As with the previous case, BB and the unbanded female must have been paired at least several days prior to clutch initiation, but perhaps not during the nestling stage of BB's first nest (Fig. 1).

Larger than average territories are typical for polygynous males of ordinarily monogamous species (e.g., Nolan 1978, Yosef et al. 1991, Breitwisch et al. 1999). The comparatively long territory (1,100 m) used by the polygynous male on Garner Run, however, likely reflected degraded water quality and not BB's polygynous status, *per se*. Garner Run is impacted by acid deposition, and such streams ordinarily have a lower density of nesting Louisiana Waterthrushes due to reduced aquatic macroinvertebrate prey density and diversity (Mulvihill 1999). It is likely, therefore, that the two females present on Garner Run

had the choice of just one territorial male. Consequently, a locally skewed sex ratio may have been the proximate cause for this instance of polygyny (Powell and Jones 1978, Smith et al. 1982, Wheelwright et al. 1992). It is possible, however, that the secondary female was associated earlier with another male who subsequently disappeared, a scenario that frequently accounts for opportunistic polygyny in monogamous birds (Smith et al. 1982, Ford 1983).

At Powdermill Run, a male waterthrush (black over orange; KO) banded as a nestling in 1999 returned on the very early date of 26 March 2000. On 28 March, he was recaptured during a territorial dispute with an unbanded male at Flag 32. From 7–20 April, KO was seen and heard singing frequently between Flags 25 and 32, often in the company of an unbanded female. The territory immediately downstream was occupied by another nesting waterthrush pair. On 21 April, we observed KO and his unbanded mate copulating near Flag 31, during which time another male waterthrush (paired status unknown) was heard singing from upstream.

We found a nest containing five eggs near Flag 26 on 6 May. During morning and afternoon nest watches on 11 May, we observed KO bringing food to Nest 26. Because the unbanded female was still incubating eggs during the early morning on 12 May, the last day that Nest 26 was known to be active, KO's food delivery probably represented a case of anticipatory feeding, commonly observed in Louisiana Waterthrushes when eggs are within a day or two of hatching (Eaton 1958, RSM unpubl. data). Nest 26 was found depredated on 16 May, but assuming the eggs had begun hatching on 12 May, the clutch was initiated no later than 25 April (Fig. 1).

On 2 May, KO was flushed up from the stream at Flag 33, a little beyond his usual territory. He flew upstream where he had a loud territorial interaction, including intense chipping and countersinging, with another male upstream of Flag 34. Over the next week, we repeatedly encountered one or two waterthrushes between Flags 33 and 37, but each time just one bird was seen well, and it was unbanded. We assumed, therefore, that the unbanded male in the territory above KO's had attracted an unbanded mate. We believe a partially completed nest found at Flag 37 on 4 May was this new pair's first attempt, but it never contained eggs. A completed nest found at Flag 33 on 13 May contained one egg the following day and a complete clutch of six eggs on 19 May (Fig. 1).

On 24 May we caught an unbanded male in a net set just upstream of Nest 33. We assumed that this male, which we banded black over yellow (KY), was the one associated with Nest 33. A short time later we caught KO and an unbanded female in a net set just downstream of Nest 33. We banded the female red over blue (RB), but at this time we were uncertain whether she was the female from Nest 33, caught while being chased out of KO's territory, or if KO and his mate from Nest 26 had simply strayed upstream out of their territory. Later that day, however, KO and an unbanded female, presumably his mate from the depredated Nest 26, were seen nest searching between Flags 29 and 32 and again copulating near Flag 31. We observed female RB entering and leaving Nest 33 during a nest watch on 25 May, and we observed KO foraging unchallenged upstream past Nest 33 on the same day. We never again saw male KY near Nest 33. However, an apparently unmated male, never clearly observed despite our continual efforts, but presumably KY, sang frequently during the succeeding weeks between Flags 37 and 42. By this time KO had extended his territory 250 m upstream, giving him an overall territory nearly twice as long as that typically held by monogamous males on Powdermill Run (Mulvihill 1999). In retrospect, we think that KO may have directly interfered with the initial nesting attempt of KY and RB (the partial nest found on 4 May at Flag 37), in the process usurping much of KY's territory and his mate.

We discovered KO and the unbanded female's renest on 1 June (Fig. 1) near Flag 29. Nest 29 contained four eggs and was found following an observation of KO and the female vigorously defending the nest site against an eastern chipmunk (*Tamias striatus*). On 1 June, the eggs in Nest 33 began hatching, and we observed KO in front of the nest carrying a small amount of food. Based on nest watches conducted over the course of the following week, KO provisioned nestlings at Nest 33 at a rate comparable to monoga-

TABLE 1. Comparison of nestling provisioning by monogamously paired Louisiana Waterthrushes on Powdermill Run (western Pennsylvania), 1997–2000, with provisioning at two nests of a polygynous male in 2000.

Variable	Nestling stage[a]	Monogamous pairs (n = 20)[b]	Polygynous male	
			Primary Nest 33	Secondary Nest 29[c]
Percent feeds by male	early	68.4	72.7	22.0
	mid	56.1	46.5	26.3
	late	51.0	64.5	—
Number of feeds by male/h	early	3.6	3.6	0.9
	mid	5.7	6.7	1.7
	late	6.1	9.8	—
Total number of feeds/h	early	5.4	4.9	4.1
	mid	10.5	14.3	6.3
	late	12.3	15.2	—

[a] Early (0-3 days), mid (4-7 days), late (8-10 days).
[b] Unweighted means based on a total of 253 h of observation.
[c] Nestlings depredated before late stage.

mous males (Table 1), nonetheless regularly appearing near Nest 29, where his unbanded mate was incubating. On at least two occasions we observed him gathering food directly in front of Nest 29 and he did so at least once while in the company of the unbanded female during one of her incubation absences. KO was not seen near Nest 29, however, during the last few days of provisioning at Nest 33, when his feeding rates were at their highest levels (Table 1).

All six nestlings from Nest 33 fledged on 11 June (Fig. 1). The eggs in Nest 29 hatched the next day. KO was not observed at Nest 29 during 3.5 h of nest watching at Nest 29 on 13 June, but he was seen feeding Nest 33 fledglings that day. On 14 June, we observed KO throughout the day providing care to fledglings from Nest 33, and he fed nestlings just three times during 4.5 h of observation at Nest 29. During three separate 1- to 2-h nest watches on 15 June, KO fed at Nest 29 a total of 10 times. However, he did not appear there for as long as 1.5 h at a time, when he was providing care to fledglings from Nest 33. On 15 June the unbanded female from Nest 29 was caught and banded blue over white (BW).

KO's rate of nestling provisioning at Nest 29 was considerably less than at his primary Nest 33 and, importantly, his level of provisioning did not increase as expected with nestling age, nor did BW compensate by increasing her feeding rate (Table 1). Overall feeding rates at Nest 29 changed little after nestling day four, when feeding rates typically increase substantially (Table 1). Although BW initially would have had to be considered the primary female in this polygynous trio, timing of the loss of her first nest clearly relegated her to secondary status in terms of KO's parental contribution. Nest 29 was last observed active on the morning of 18 June, at which time the nestlings appeared noticeably underdeveloped for their age (six days); the nest was found depredated on the following morning. We did not observe BW again after the loss of Nest 29. We observed KO and RB feeding their fledglings in separate brood units until at least 23 June.

Benefits associated with biparental care for the reproductive success of both sexes is believed to be the principal factor promoting monogamy in territorial altricial birds (Wittenberger and Tilson 1980). Monogamous male waterthrushes typically contribute the larger share of nestling provisioning, especially during the early nestling stage (Table 1). Females ordinarily spend the majority of time at this stage brooding their young (Robinson 1995), which presumably do not develop homeothermy for several days after hatching (Hann 1937). KO's contribution at Nest 29 was minimal during the critical early nestling period (Table 1). We did not observe KO feed newly hatched nestlings at his secondary nest until two days posthatching, and then at only comparatively very low rates (Table 1). In contrast, at all nestling stages KO provisioned his primary nest at rates nearly equal to monogamous males (Table 1), and he subse-

quently also provided substantial postfledging care to that brood. If, as preliminary observations of several broods indicate, Louisiana Waterthrushes completely divide their brood immediately upon fledging (AC and LQ unpubl. data), then this further increases the importance of biparental care to nesting success in this species.

Secondary nesting female wood warblers sometimes increase their overall feeding rate to compensate for reduced male contribution (e.g., Blackpoll Warbler, Eliason 1986; Yellow Warbler, *Dendroica petechia*, Hobson and Sealy 1989), however, BW did not (Table 1), and the development of her nestlings appeared to be affected negatively. A similar observation was made at the second nest of a bigamous Black-throated Blue Warbler (Petit et al. 1988). In that case, retarded development of the nestlings was believed to have contributed to their inability to escape squirrel predation when they were within a day of fledging. Given that we found Nest 29 as a result of the vigorous and successful joint nest defense by KO and BW against a chipmunk just one day before KO's primary nest hatched (Fig. 1), KO's preoccupation with recent fledglings from Nest 33 may have contributed to the depredation of nestlings in his later hatched Nest 29. Thus, one of the principal "costs of sharing" (Bensch 1997) associated with polygyny, reduced male parental care at secondary nests, actually was borne by BW, KO's primary (or first-mated) female due to her earlier nest loss.

In the Powdermill Run case, costs of sharing may not have been limited to reduced male assistance with parental care; they also may have included a substantial protraction of the renesting interval for the first mated female (Czapka and Johnson 2000). Waterthrushes are persistent renesters following nesting failure at any stage, not infrequently making as many as three attempts during a season (RSM unpubl. data), and the interval between these attempts typically is just 5–6 days, approximately the physiological minimum for oocyte maturation (Scott et al. 1987). We estimated that the interval between nesting attempts for female BW was 12–16 days (Fig. 1). Because of both reduced parental care and delayed renesting, the possibility of losing status following nest loss represents a clear potential cost of sharing for primary females who might, therefore, be selected to interfere with a male's ability to form additional pair bonds (Temrin 1991, Bensch 1997). On the other hand, the possibility of attaining primary status in the current nesting season, or perhaps in future nesting seasons (Clemmons 1994), may at least partially compensate female waterthrushes that choose to mate with already mated males.

In the Powdermill Run case, polygyny seemed to be a direct result of the sustained aggressive take over by one male of the territory (and possibly also the mate) of another. KO's behavior in acquiring a comparatively very large territory and an additional mate in the presence of competition was very similar to that observed for males having naturally or experimentally elevated plasma levels of testosterone (Wingfield 1984, Wingfield et al. 1987). This suggested that KO's behavior itself was the proximate cause of polygyny in this case. The possibility that KO had an innate tendency to pursue this mating strategy was strengthened when he was confirmed polygynous again in 2001.

We observed fewer details of KO's breeding activity during 2001, but he was once again the first waterthrush to return to territory on Powdermill Run. Female BW, although not seen after their second nest failure the year before, was again KO's primary female, but this time their initial nesting attempt near Flag 34 was successful; we observed KO feeding a newly fledged young from Nest 34 on 29 May (Fig. 1). Although we never found the nest, a successful nesting attempt with a second color-banded female (green over green; GG) was confirmed when we observed KO and GG feeding recently fledged young near Flag 29 on 2 July. Estimated dates of nesting indicate that there was much less overlap between KO's two nests during 2001, the chronologies of which were similar to the observed nests of polygynous males on Laurel Run and Garner Run (Fig. 1). We do not know, however, if there had been an earlier nesting attempt by KO and GG, which would have resulted in considerably more overlap between broods, perhaps similar to his nestings in 2000.

Regardless of the specific circumstances leading to it, the nestling phase of the later-

hatched nests in three of the four observed polygynous pairings at most overlapped only during the late stages of fledgling care of the primary nests (Fig. 1). Although we did not observe nest provisioning behavior in these cases, it is likely that the costs of sharing for females at the secondary nests were much less compared to the first observed case on Powdermill Run (Table 1). Importantly, any mitigation of sharing costs from a reduction of nesting overlap is contingent upon comparatively very late initiation of any secondary nests. The initiation dates for the secondary nests at Laurel Run (29 May), Garner Run (3 June), and Powdermill Run in 2001 (30 May) were among the latest that we have observed during our study. In addition, because of protraction of the renesting interval, the second nest of the primary female on Powdermill Run in 2000 also was initiated on the comparatively late date of 27 May. During our study, just over 12% of all waterthrush nesting attempts were initiated after 26 May. Several possible costs of late breeding, also considered in the context of constraints on double brooding in the species (RSM unpubl. data), might similarly negate any advantages of staggered nesting for polygynous waterthrushes; these include reliance on off-peak food resources, delayed molt, molt-breeding overlap, and delayed migration.

In summary, because our observations spanned several nesting seasons and numerous study sites, we are confident in concluding that polygyny is very rare in Pennsylvania populations of the Louisiana Waterthrush. We believe that this likely stems from greater selective advantages for both sexes related to biparental nest defense and care of young, as well as short renesting intervals following nest loss. Given the degree to which monogamy appears to be enforced in this species, some theories predict that male waterthrushes should be selected to pursue a mixed mating strategy involving extrapair copulations (EPCs; Trivers 1972, Ford 1983). Extraterritorial intrusions, a behavioral correlate of the EPC strategy (Ford 1983, Pitcher and Stutchbury 2000), have been observed in waterthrushes many times during our study, but the occurrence and/or extent of extrapair fertilizations in the species remains to be determined.

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ROADSIDE HAWK BREEDING ECOLOGY IN FOREST AND FARMING LANDSCAPES

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ABSTRACT.—We compared breeding ecology, density, and reproductive success of Roadside Hawks (*Buteo magnirostris*) in two Guatemalan study areas during 1993 and 1994. Primary forest supported 1.15 territorial pairs/km^2 whereas a slash-and-burn farming landscape supported 1.41 territorial pairs/km^2. All nests (n = 32) were in emergent trees. Hawks nested selectively in low canopy, seasonally inundated primary forest, and spacing of nests was related to the distribution of this forest type. Pairs did not nest selectively in a particular habitat in the farming landscape, but nested in isolated, emergent trees. Nest success (proportion of attempts that produced ≥1 fledgling) was 0.17 in the forested area and 0.30 in the farming landscape. Productivity (fledglings per territorial pair) was 0.08 in the forest and 0.32 in the farming landscape. Incidence of non-nesting by territorial pairs was greater in the forest (50%) than in the farming area (20%). The overall rate of nesting by territorial pairs was 65%. The most frequently identified cause of nest failure in the farming landscape was human persecution, while in the forest it was predation. Prey delivery rates did not differ significantly between habitats.
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Habitat modification by humans continues to affect a growing portion of the forested tropics. Slash-and-burn or shifting cultivation is a prevalent agent of forest alteration in many areas (Myers 1980). This type of farming involves cutting, burning, and cultivation of the forest for 1–4 years followed by leaving the area fallow for several years before it is again farmed or converted to pasture (Peters and Neuenschwander 1988). This activity produces a constantly changing mosaic of clear cuts, crop fields, woody second growth, pastures, abandoned shrublands, monocultures of cosmopolitan species such as bracken fern (*Pteridium aquilinum*), and mature forest fragments. These habitat changes may affect availability of nest sites (Newton 1992, Janes 1994), food, and important features of hunting habitat for raptors as well as their breeding density, productivity, and survivorship (Gargett 1975, Newton et al. 1986, Watson et al. 1992). Direct human persecution may be an additional important mortality source (Thiollay 1984, Alvarez-Cordero 1996).

It is unknown how the dynamic nature of slash-and-burn farming landscapes affects the demography of raptors and which of several potential mechanisms of impact may be important for different raptor species. While some studies have described shifts in composition of tropical raptor communities in concert with different land uses (Thiollay 1993, 1996; Jullien and Thiollay 1996), no study, to our knowledge, has examined the demographic consequences of habitat alteration for any tropical forest raptor. Such knowledge might aid in management of tropical agroecosystems to sustain intact raptor communities.

We selected the abundant and conspicuous Roadside Hawk (*Buteo magnirostris*) as a subject for studying the effects of slash-and-burn farming on a tropical raptor. Wetmore (1965), Brown and Amadon (1968), and Bierregaard (1994) provided summary accounts of Roadside Hawk biology, and other authors presented brief information on diet and hunting (Haverschmidt 1962, Beltzer 1990), and on systematics and morphology (Hellmayr and Conover 1949, Friedmann 1950, Johnson and Peeters 1963, Blake 1977). These hawks often are associated with thinned forests, forest edges, and natural or anthropogenic clearings (Bierregaard 1994). Earlier work at our study site revealed Roadside Hawks nesting in primary forest (Vásquez and Reyes 1992) and found these raptors common in both primary forest and human-modified habitats (Whitacre et al. 1992a, 1992b). It was not known, however, whether habitat alteration was beneficial

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or detrimental to the species. Our objective was to document aspects of Roadside Hawk breeding ecology, with emphasis on comparing these attributes in primary forest and a slash-and-burn farming environment.

METHODS

Study area.—Our two study sites were 25 km apart in and near Tikal National Park (17° 11′ N, 89° 48′ W), Guatemala. Topography is relatively level with low, rolling hills 160–350 m in elevation. Mean annual rainfall is 136 cm with a pronounced dry season February to May. There are no permanent streams in the area; during the dry season, surface water is found only in a few water holes. The 576-km² Tikal National Park supports mostly unlogged, mid-height to tall semideciduous tropical forest (Pennington and Sarukhan 1968). Forest vegetation varies as a continuum along a topographic and soil type gradient from well-drained to poorly drained sites (Schulze and Whitacre 1999). We focused on the readily recognizable "bajo" and "upland" forest extremes. The bajo forest type includes Schulze and Whitacre's (1999) hill-base, sabal, transitional, and scrub-swamp forest types, all of which grow in low-lying areas; the scrub swamp types retain standing water during the rainy season. These lowground forest types feature low (10–17 m), relatively open canopies with a few 15–25 m emergent trees and a dense, vine rich understory. Upland forests occur on well-drained sites and are characterized by complex structure, a tall (20–30 m), closed canopy, and a thin, well-shaded understory (Schulze and Whitacre 1999).

The primary forest site, near the center of Tikal National Park, was an 8.25-km² (5 × 1.65 km) area containing transects every 100 m, and was imbedded in an immense area of mature forest (>15,000 km²). Bajo forest occurred as small patches in swales surrounded by upland forest on gentle ridges. A dirt road passed through one end of the area. The slash-and-burn study site (8 km², 4 × 2 km) was 10 km south of the Park, within an extensive area of human-modified habitat. This study area contained disturbed fragments of primary upland and bajo forest, crop fields (mostly corn), pastures, clear cuts, bracken fern monocultures, and land in successional stages from low brush to 10-m second growth. Less than 10% of the study site was covered by mature forest remnants. Several livestock watering holes dotted the landscape and an asphalt road passed through the area.

Breeding density.—We systematically searched for Roadside Hawks in each habitat from March through May. Each transect was walked twice, on different days, at different times (morning and late afternoon) and by different individuals. We stopped every 100 m for 1 min to listen and look for Roadside Hawks, noting all activity on a map. We searched a new area each day until the entire study site was completed. In addition to the systematic searches, we searched both habitats throughout the breeding season to locate all territorial pairs.

Areas of Roadside Hawk activity were revisited by 2–3 persons to find a nest or verify non-nesting. Roadside Hawks often vocalized from the nest or perch tree for a brief period after sunrise. Before dawn, one person climbed a tree using climbing equipment and waited for Roadside Hawk activity. The other individuals searched on foot and waited for hawks to call ≥3 times from the same tree before approaching. Nest trees were not flagged nor approached again except as noted below. Once we located all nests and pairs each year, we searched each area again and broadcast Roadside Hawk defense calls using Johnny Stewart Game and Animal Callers (Waco, Texas). Nesting and territorial pairs responded to the broadcasts throughout the breeding season by issuing defense calls, aerial displays, and/or perching in trees near the game caller; no additional pairs or nests were found through these efforts.

Although few adults were banded, we could distinguish different pairs by their reliable occurrence in small, specific portions of the study areas. Pairs were omitted from density calculations if more than half their territory was outside the study site boundary, and pairs with nests along the boundary (e.g., 10 m inside or outside) were regarded as having half their territory within the site. We also estimated density for the forest site using a plotless, polygon-based method. A convex polygon was extended to half the mean internest distance around all nest sites, and the resultant area was divided by the number of territories contained therein (Watson 1990, Berkelman 1993). We calculated mean internest distance among neighbors using the minimum spanning tree method (Selås 1997), and compared the two study sites using the Mann-Whitney *U*-test (Sokal and Rohlf 1981).

Productivity.—We checked each territorial pair every 3–6 days throughout the breeding season to record territory occupancy, nesting incidence, and nest success. Nesting pairs were those that built a nest and laid ≥1 egg. Non-nesting territorial pairs defended a territory but did not lay an egg (nor did they complete a nest). We climbed a nearby tree or the nest tree to record clutch size after a female began incubating. When a nest failed, we searched the area for evidence of the cause of failure. We assessed productivity by visiting nests during June and July and counting fledged young. Nest success was the proportion of nesting attempts that produced ≥1 fledgling. Productivity was the number of young fledged per territorial pair, including non-nesting pairs (Steenhof 1986). This measure better assesses reproduction than some alternative measures, because it includes all types of failure, including territorial pairs' failure to nest (Newton 1979).

Prey delivery rates.—We observed four slash-and-burn nests for 229.5 h and two forest nests for 137.4 h from April to June 1994 to examine prey delivery rates. We observed from blinds on the ground and in trees ≥30 m from nests, using 10× binoculars and a spotting scope. We observed nests from dawn to dusk (13 h), changing observers at noon.

Nest site and habitat characteristics.—We measured several habitat variables around each nest once a nest failed or young fledged. We determined latitude and longitude at all nest trees and study site corners using a TransPak II Global Positioning System (Trimble Navigation, Sunnyvale, California), recording the mean of ≥20 readings. We measured macrohabitat variables at 20-m intervals along 300-m transects in the four cardinal directions from each nest tree. At each of these intervals we also noted habitat type (e.g., bajo forest, pasture, crop field) and, because of the variability in the slash-and-burn habitat, we took three canopy height measurements (Haga altimeter; Forestry Suppliers, Jackson, Mississippi) facing each cardinal direction from the same position. We used linear regression to examine whether canopy height increased with distance from nest sites. We measured the following microhabitat variables at each nest: nest tree species, height, and diameter (dbh); nest height, length, and width; and distance to the nearest tree of similar (equal or greater) height. We measured mean canopy height 5 m in each cardinal direction from the nest tree.

We measured the same variables at 40 random points to characterize potential nesting habitat in each study site; a random number generator selected UTM coordinates for sampling. Once the approximate point was located, we selected the nearest tree >10 cm in diameter and took measurements as described above. We compared habitat characteristics at nest sites and random points using Mann-Whitney *U*-tests.

We mapped forest types throughout the primary forest site to examine whether Roadside Hawks nested disproportionately often in a specific forest type. We walked 84.15 km of transects within the area (51 1.65-km transects spaced 100 m apart), and noted the forest type every 50 m. Forest at each point was designated upland, bajo, or transitional, after Schulze and Whitacre (1999). We used a *G*-test (Sokal and Rohlf 1981) to determine whether Roadside Hawks nested selectively in bajo or upland forest compared to the availability of these habitats in the forest site. We did not map cover types in the slash-and-burn site due to continued disturbance; here, selectivity with regard to nest habitat was evaluated using the 40 random points described above.

All statistical tests were performed using SAS Version 6 (SAS Institute, Inc. 1989). Significance tests were performed at $\alpha = 0.05$, with critical values adjusted where appropriate using a sequential Bonferroni procedure (Rice 1989).

RESULTS

Density.—We determined locations of 14 territories in the forest area, with ≤13 occupied during a given year. During 1993, five of 13 pairs (38.5%) nested, while during 1994, seven of 11 pairs (63.6%) nested. There were 10 pairs within the site's boundaries during 1993 and nine during 1994, for a mean density of 9.5 territorial pairs/8.25 km² (1.15 territorial pairs/km²). A polygon-based method gave a density of 1.18 territorial pairs/km², very similar to the above result.

We also found 14 territories in the slash-and-burn area, of which 12 were occupied in 1993 and 13 in 1994. Unlike the forest site, percent of territorial pairs that nested differed little between years; in 1993 10 of 12 territorial pairs (83.3%) nested, while in 1994, 10 of 13 pairs (76.9%) nested. Eliminating partial territories, the mean density was 11.25 territorial pairs/8 km² (1.41 territorial pairs/km²). For nesting pairs, the 2-year mean density for the forest site was 6 nesting pairs/8.25 km² and 10 nesting pairs/8 km² in the farming landscape.

We observed 17 territorial pairs that copulated, courted, carried sticks, and defended territories, but did not finish nest building. We saw these pairs attacking conspecifics and other raptors and/or displaying in their territorial areas throughout the breeding season. All non-nesting territorial birds ($n = 34$) had adult plumage and yellow irides, an adult characteristic, hence presumably were adults and physiologically capable of breeding. The forest site had a higher incidence of non-nesting among territorial pairs (50%, 12 of 24) than did the slash-and-burn area (20%, 5 of 25; $G = 4.971$, df = 1, $P = 0.026$; Table 1).

Nearest-neighbor distances between occupied nest sites differed between the two study areas (Mann-Whitney *U*-test; $U = 150$, $P = 0.005$). Internest distances in the forest were extremely variable, ranging from 494–2,580 m (mean = 1,156 m ± 750 SD, $n = 10$), and reflected the distance between areas of bajo forest. Nest sites in the farming landscape were closer together (mean = 480 m ± 193 SD, $n = 11$), with distances between occupied nest sites ranging from 252–904 m.

Productivity.—We recorded 20 one-egg and 8 two-egg clutches, with a mean clutch size of 1.29 ± 0.46 SD ($n = 28$). Six of 17 nests (35%) in the slash-and-burn area had two-egg clutches, compared to two of 11 nests (18%) in the forest ($G = 0.998$, df = 1, $P = 0.32$).

Productivity and nest success were low. Combining all data, productivity was 0.2 fledglings per territorial pair per year, and only 25% of nesting efforts resulted in ≥1 fledged young (Table 1). Low productivity was due in

TABLE 1. Roadside Hawk nesting in two habitats, Petén, Guatemala.

Variable	Forest			Slash-and-burn farming		
	1993	1994	Total	1993	1994	Total
Number of non-nesting pairs	8	4	12	2	3	5
Number of nesting pairs	5	7	12	10	10	20
Number of successful nests	1	1	2	4	2	6
Number of nests with eggs that failed	3	5	8	4	4	8
Number of nests with young that failed	1	1	2	2	4	6
Number of fledglings produced	1	1	2	5	3	8

part to a high incidence (35%) of non-nesting by territorial pairs. In the forest, mean productivity was 0.08 fledglings/territorial pair, and 0.17 nests were successful per nesting attempt (Table 1). Mean productivity in the slash-and-burn area was 0.32 fledglings/territorial pair, and 0.30 nests were successful per nesting attempt.

Nest failure was common in the forest, with egg and nestling mortality occurring both years (Table 1), resulting from wind (n = 2) and predation (n = 3). Predation also was suspected at four additional nests where eggshell fragments were found or eggs disappeared. Most evidence (claw marks and fur on nest trees) implicated mammals, and a tayra (Mustelidae: *Eira barbara*) was sighted near one nest. In the slash-and-burn area, nest failure was slightly more common during the egg stage (n = 8) than the nestling stage (n = 6; Table 1), and human persecution (n = 4) was the most frequently identified cause of nest failure. Two nest trees were cut down, leading to premature fledging in one case and nestling death in the other. Another nestling disappeared from its nest and machete marks were found on the tree. We observed two boys playing with sling shots at another nest and by noon the nest had fallen and the egg was gone. We found no evidence of the cause at four other nests where nestlings disappeared. Study pairs in both habitats (n = 24) whose nests failed defended territories throughout the breeding season, but did not renest. At nests outside the study sites, we observed two cases of apparent renesting after initial failure, but these did not involve marked birds.

We observed one case each of cannibalism and siblicide in the forest site. In 1993 a Roadside Hawk in adult plumage but with dark irides (probably a yearling) entered a nest and ate a 14-day old chick. In 1994, we observed siblicide in a two-chick brood where the larger nestling attacked its smaller sibling until the latter fell from the nest. We suspected siblicide at another forest nest where one nestling disappeared and the other fledged two weeks later. We saw no aggression between nestlings while monitoring five two-chick broods in the slash-and-burn area.

Prey delivery.—Reptiles (57%) and amphibians (24%) comprised most prey items at nests, with mammals representing 8%, insects 9%, and birds 2% (n = 140 prey items; Panasci and Whitacre 2000). Per-chick prey delivery rates did not differ significantly between nests in the forest and farming habitats (Mann-Whitney U-test; U = 9, P = 0.49), nor between one- and two-chick broods (U = 10, P = 1.00). The mean prey delivery rate at forest nests was 0.311 prey/h/chick ± 0.068 SD (n = 2 nests), and at slash-and-burn nests was 0.275 ± 0.134 (n = 4 nests). The mean delivery rate at one-chick nests was 0.264 prey/h/chick ± 0.095 SD (n = 3 nests), and at two-chick nests was 0.311 ± 0.140 (n = 3 nests). We detected no significant difference in the per-nest total prey delivery rates between nests in the two habitats (Mann-Whitney U-test; U = 5, P = 0.49). The mean rate at forest nests was 0.366 prey/h/nest ± 0.010 SD (n = 2 nests), and at slash-and-burn nests was 0.439 ± 0.080 (n = 4 nests).

Nest sites and habitat.—We found 32 Roadside Hawk nests during 1993 and 1994. All were flat, platform nests loosely built of sticks. All 12 forest nests and 12 of 20 slash-and-burn nests were concealed from above and/or below by vine tangles. Mean nest dimensions were 34.7 cm in length and 26.3 cm in width (n = 16), and all contained some green leaves in a slight depression in the cen-

ter. Roadside Hawks nested in emergent trees in both habitats (Table 2). The mean height of nest trees in the forest site was nearly twice the height of the surrounding canopy. Roadside Hawks nested at significantly lower heights in the slash-and-burn habitat, and in shorter, smaller diameter trees, surrounded by shorter vegetation (Table 2). However, all 20 slash-and-burn nests were in emergent trees as well, and nests in both habitats had a mean height of 7 m above the surrounding canopy.

Roadside Hawks in the primary forest site nested selectively in low-stature bajo forest, avoiding tall, upland forest. All nests (n = 12) were in bajo or transitional forest, even though these forest types comprised only 10.3 and 5.4% of the forest study site, respectively (the remaining 84.3% of the site supporting upland forest). Nests were in bajo forest more often than expected; of 40 random points, seven were in bajo forest and 33 in upland forest (G = 51.56, df = 1, P = 0.0001). In addition, forest nest sites differed in habitat from random points. Roadside Hawk nests were in taller, larger diameter trees, in forest with lower canopy height, and in trees with a greater distance to a tree of similar height, relative to the random sample (Table 2). Canopy height for the forest site increased with distance from the nest (over a 300-m distance at 20-m intervals; linear regression: r^2 = 0.916, F = 141, P = 0.0001), reflecting that forest nests were in areas of low canopy bajo forest surrounded by a matrix of taller, upland forest.

Values of microhabitat variables near slash-and-burn nests did not differ significantly from those at random points except that hawks nested in larger trees (Table 2). Nests in the slash-and-burn site were not detectably associated with a certain forest type, and occurred in isolated groves amidst cattle pastures, crop fields (n = 12), or woody successional vegetation (n = 8).

Reuse of nest sites between years was rare in the forest and not observed at all in the slash-and-burn area. In the forest, two 1994 nests were built in trees where nests had failed during 1993; in one case the pair reused the previous year's nest; all other 1994 nests were in trees different than those used the previous year. In addition, one 1994 forest nest tree had been used by nesting Gray-headed Kites (*Leptodon cayanensis*) the previous year. Of the

TABLE 2. Roadside Hawk nest site characteristics in two habitats, Petén, Guatemala, 1993 and 1994. Values are mean ± SD.

	Slash-and-burn farming			Forest			
Variable	Nests (n = 20)	Random (n = 40)	P^a nests versus random	Nests (n = 12)	Random (n = 40)	P^a nests versus random	P^a forest versus farming
Nest height (m)	10.63 ± 3.30			20.26 ± 3.01			0.0001
Tree height (m)	12.96 ± 4.22	11.24 ± 7.19	0.1468	23.42 ± 3.01	17.07 ± 2.41	0.0001	0.0001
Mean canopy height (m)	3.77 ± 3.16	5.45 ± 6.17	0.6675	12.58 ± 3.45	17.31 ± 2.31	0.0001	0.0001
Nest tree DBH (cm)	25.28 ± 13.15	17.37 ± 15.23	0.0026	53.66 ± 23.93	34.44 ± 15.16	0.0068	0.0005
Distance to a tree of similar height (m)	7.29 ± 7.64	5.78 ± 4.48	0.6436	9.56 ± 6.59	5.20 ± 3.35	0.0231	0.1240

[a] Mann-Whitney U-tests. Probabilities Bonferroni adjusted.

eight territories where pairs nested during 1993 in the slash-and-burn site, each was occupied during 1994 but nests were located in different trees; the mean distance between 1993 and 1994 nest sites within a given territory was 231 m ± 120 SD (range = 55–443 m, n = 8).

DISCUSSION

The low productivity we observed resulted from small clutch size, high rates of nest failure, and relatively high rates of non-nesting. The annual productivity values we found were very low for a raptor population not adversely affected by environmental contaminants (Newton 1979). Our productivity value is low even by tropical standards. In temperate zone accipitrids (n = 15 species), mean productivity was 1.23 fledglings/territorial pair, whereas tropical accipitrids (n = 11 species) had a mean productivity of 0.51 fledglings/territorial pair (as calculated from Newton 1979: Table 23).

The difference in productivity between temperate and tropical raptors (Newton 1979) was due largely to the larger mean clutch size of temperate raptors (2.8, n = 14 species) compared to tropical raptors (1.5, n = 12 species). A two-egg clutch size is reported for Roadside Hawks from Costa Rica northward (Howell and Webb 1995, Smithe 1966, Stiles and Janzen 1983). Based on 127 museum egg sets from Mexico, Central, and South America, mean clutch size for Roadside Hawks is 1.92 eggs ± 0.41 SDs (16 one-egg, 105 two-egg, and six three-egg sets; T. A. Panasci unpubl. data), compared to the mean clutch size of 1.29 eggs that we found at Tikal. We can offer no explanation for the smaller clutch size we found; more data are needed to evaluate whether this finding is typical for this region.

Again using Newton's (1979) data, among temperate zone accipitrids (n = 15 species), 84% of territorial pairs nested (laid eggs), while in tropical accipitrids (n = 12 species, all African), 70% of territorial pairs nested (U = 144.5, P = 0.008). With 65% of territorial pairs nesting, Roadside Hawks resemble the tropical raptors cited above. However, the 25% nest success we documented was very low compared to both temperate zone (68.3% ± 1.75 SE, n = 17) and tropical accipitrids (65.9% ± 3.68 SE, n = 12; Newton 1979: Table 23). Vásquez and Reyes (1992) reported two fledglings from six nests at Tikal, for a nest success of 33% and a productivity of 0.30 fledglings per nesting attempt. It is possible that our climbing to some nests to verify clutch size may have contributed to nest failure; 5 of 13 nests to which we climbed failed while only 3 of 19 nests to which we did not climb failed.

Limited nest sites and a more diverse raptor assemblage offer one potential explanation why the incidence of non-nesting by territorial pairs of Roadside Hawks was greater in the mature forest than in the farming landscape. While a few raptor species at Tikal were more abundant in the farming landscape than in the primary forest, many species were more abundant in the forest than in the farming landscape (Whitacre et al. 1992a, 1992b). The net result is that raptor species richness was much greater in the primary forest than in the farming landscape, possibly leading to greater interspecific competition. Nest sites did not appear to be a limiting resource for Roadside Hawks in the slash-and-burn site; the hawks changed nest sites each year and used trees fairly typical of those available. That two 1993 nest trees in the forest were used again during 1994, whereas no nest sites were reused in the slash-and-burn area, supports the hypothesis that nest sites were more limiting in the forest than in the farming landscape. Moreover, the change in possession of a nest tree that we noted between Gray-headed Kites and Roadside Hawks, and our finding that many raptor species at Tikal used emergent trees similar to those used by Roadside Hawks (Whitacre et al. 1992a, 1992b) point to the possibility that nest site competition may occur in the primary forest.

Primary forest and human-modified habitats in our study differed markedly in vegetation structure, and likely also differed in prey resources. However, prey delivery rates to nests in the two habitats were similar. Prey delivery rates may in some cases be a good index of habitat quality and food resources (Bennetts et al. 1994). However, a difference in prey availability between habitats might result in different proportions of territorial pairs nesting. Consequently, the lack of difference in prey delivery rates at nests in the two hab-

itats is not convincing evidence of similar foraging conditions.

Roadside Hawks consistently selected emergent nest trees from those available. In the farming landscape this was not associated with any discernible selection of a particular vegetation type. However, in the mature forest Roadside Hawks showed strong selectivity of low canopy bajo forest as nest habitat, and avoided nesting in the tall, closed canopy forest that covered 80% of the forest site. Robinson (1994) also reported that Roadside Hawks nested in isolated trees in Peru. Isolated and emergent trees, having minimal connection to adjacent canopy, may provide some safety from climbing predators.

Conservation implications.—Thiollay (1984) and Alvarez-Cordero (1996) reported that tropical forest raptors in some cases experienced high mortality due to direct persecution by humans. Even though Roadside Hawks in our study successfully nested in a slash-and-burn farming landscape, human persecution was the most frequently identified cause of nest failure there. This suggests that for other, more sensitive raptor species, persecution may be a determinant of their success in human-modified environments.

Roadside Hawks did not seem negatively affected by habitat alteration in the farming landscape. Although dramatic changes in vegetative cover occurred each breeding season in the slash-and-burn site, locations and occupancy of Roadside Hawk territories remained stable. In addition, incidence of nesting by territorial pairs, nest success, and productivity all were greater in the farming landscape than in primary forest. These results suggest that land use practices typical of slash-and-burn farming did not negatively affect our Roadside Hawk study population. Our results suggest the farming landscape at Tikal may have been a more hospitable environment for Roadside Hawks than the mature forest. This is not surprising, given that these raptors are widely known as habitat generalists (Bierregaard 1994, Panasci and Whitacre 2000). Of greater conservation importance was the noticeable amount of nest failure resulting from direct human persecution. Reducing persecution through education may increase the potential of tropical agroecosystems to retain a maximal portion of their indigenous raptor faunas.

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FOOD SUPPLY AND PARENTAL FEEDING RATES OF HOODED WARBLERS IN FOREST FRAGMENTS

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ABSTRACT.—We tested whether Hooded Warblers (*Wilsonia citrina*) experienced a smaller food supply in small versus large forest fragments in northwestern Pennsylvania. Using 16 fragments that ranged in size from 0.7 to 214 ha, we videotaped parental feeding rates to nestlings in 35 nests and sampled arthropod abundance on 24 breeding territories. Contrary to our predictions, neither feeding rate per nestling nor arthropod abundance on breeding territories was significantly less in small (<4 ha) versus large (>150 ha) fragments. Brood loss due to starvation was rare and overall nest success was not significantly less in small fragments. Similarly, prey size delivered to nestlings and arthropod size sampled on territories did not differ significantly between fragment size classes. We conclude that Hooded Warblers breeding within small forest fragments in the northwest Pennsylvania landscape do not suffer from a relatively small food supply. *Received 20 February 2001, accepted 21 March 2002.*

Research on fragmentation of temperate forests and food availability has suggested that small forest fragments contain less prey biomass than large forests. Burke and Nol (1998) found that invertebrate biomass in leaf litter was 10 to 36 times lower in Ovenbird (*Seiurus aurocapillus*) territories located in forests with >20 ha core area (area greater than 100 m from the edge). Furthermore, randomly located quadrants in small fragments contained less than half the invertebrate biomass compared to random quadrants in large forests. In Australia, Zanette et al. (2000) found a similar reduction in food for Eastern Yellow Robins (*Eopsaltria australis*); the abundance of surface-dwelling invertebrates in two small (<55 ha) forests was half that of two large (>400 ha) forests.

Because food can limit reproductive success in passerines (Martin 1987, Rodenhouse and Holmes 1992), reductions of food caused by fragmentation should have negative consequences on reproductive success. Zanette et al. (2000) found that Eastern Yellow Robins breeding in small forests had smaller eggs and nestlings compared to birds nesting in larger forests. However, in Europe, Great Tits (*Parus major*) and Blue Tits (*P. caeruleus*) occupying small fragments had feeding rates and nesting success similar to pairs in larger forests (Nur et al. 1998).

Hooded Warblers (*Wilsonia citrina*) are small, insectivorous, Neotropical migrants with a body mass of about 11 g. They are a good species for studying the relationship of forest fragmentation and parental feeding as they are considered an area sensitive, forest interior species (Freemark and Collins 1992), and their low nests are easily located and monitored. Hooded Warblers are socially monogamous and exhibit biparental care (Evans Ogden and Stutchbury 1997). They primarily glean, hawk, and hover for a wide variety of arthropods in the understory layer of the forest (Bent 1953, Evans Ogden and Stutchbury 1994; BJMS pers. obs.) with males and females using a variety of foraging heights on the breeding grounds, particularly when provisioning young.

In this study, we tested whether feeding rate and prey size in Hooded Warbler parents were associated with fragment size in northwest Pennsylvania. Using 16 forest fragments ranging in size from 0.7 to 214 ha we videotaped parental provisioning to nestlings in 35 nests. In addition, we sampled arthropods on 24 breeding territories to determine whether arthropod abundance was related to fragment size.

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METHODS

We collected data from May through July, 1999 and 2000, in 16 forest fragments within Crawford County, northwestern Pennsylvania (centered on 41° 46′N, 79° 56′W). Forests were mature to semimature mixed hardwood deciduous and were isolated, or at most connected to other forests by narrow (<40 m wide) corridors. The mean distance to the nearest forest was 110 m (range 40–250 m). Land use between forest patches was mainly cultivated or fallow farm fields. Fragments were classified to size: small (0.7–4.0 ha, n = 12 fragments) or large (>150 ha, n = 4 fragments). In the large fragments the mean distance from the edge for all territories and nests was 257.1 m ± 145.6 SD, with 80% of the nests >100 m from the forest edge. In each fragment, 70–80% of adult birds were captured in mist nets and banded with a unique combination of plastic color bands and USGS-BRD aluminum bands.

We located nests at the nest-building, egg-laying, and incubation stages by following the sound of female vocalizations to the nest. Once located, nests were checked every 2–3 days to document hatching rates and nest success. Fledging success was calculated using the ratio of nestlings fledged to nestlings hatched. Because Brown-headed Cowbird (*Molothrus ater*) nestlings are likely to require additional food, all parasitic eggs were removed prior to hatching. Mean brood size for small fragments was 2.62 ± 1.12 SD and for large fragments 3.10 ± 1.00 SD after the removal of cowbird eggs. These means did not differ significantly (U-test: U = 1.03, Z (adjusted) = 1.26, P = 0.21) and in our analysis we controlled for the number of nestlings per brood by measuring feeding rates as feeding rate per nestling (feeding trips/h/nestling). After hatching, nests were monitored via video recording to determine feeding rates and prey sizes. We placed video cameras 1.0–1.5 m from the nest and feeding behavior was recorded using 2-h tapes. Parents fed at least once during all of our filming sessions. Each nest was recorded for a total of 4–6 h between 06:30 and 17:00. Evans Ogden (1994) found that time of day was not associated with feeding rates in Hooded Warblers at our study site in northwestern Pennsylvania. Hooded Warbler young fledge from the nest when they are approximately 9 days old (Evans Ogden and Stutchbury 1997) and all taping took place 5–7 days after hatching. Filming was conducted over multiple days in order to attain a mean feeding rate. All nests were taped over two of the three possible days (5–7 days old), and there was no systematic bias in age of nestling and fragment size.

While viewing the tapes, we estimated prey size in relation to bill size (Simmons and Martin 1990). Hooded Warblers have a bill size of approximately 9 mm and prey items were placed into one of five prey size categories: (1) <5 mm (2) 5–9 mm (3) 10–19 mm (4) 20–30 mm and (5) >30 mm. Hooded Warblers generally are single prey loaders; however, in the event that multiple prey items were delivered during one feeding trip, each prey item was individually placed into one of the prey size categories. After samples were categorized by size, we determined median prey size. Medians were used as a way to minimize the effect of extremely small or large prey outliers, as prey sizes varied widely. In addition, prey size was quantified as a percentage of prey items longer than 20 mm. Hooded warblers feed on a wide variety of arthropod prey including flies, ants, wasps, beetles, moths and their larvae, caddisflies, and spiders (Bent 1953; BJMS pers. obs.), therefore all types of prey were considered in our analysis.

To compliment parental feeding data and to examine the association of fragmentation with available food on breeding territories, we collected arthropod samples by sweep netting 24 breeding territories; 12 of these territories also were sampled for parental feeding rates. Using methodology similar to Young (1994), we walked along 30- to 40-m transects extending from the center of the territory. Transects were located on each of the cardinal axes (N, S, E, W) and 30 sweeps, alternating between high and low, were taken along each of the four transects. We collected samples on sunny days within a 2-week period between 08:00 and 16:00, June 2000. Samples were emptied into plastic bags at the end of each transect and then frozen. We sorted the arthropods into vials containing isopropyl alcohol. Arthropods were placed into one of five size classes used for parental feeding. We calculated total arthropod abundance as well as mean and median arthropod sizes.

Most (15 of 21) of the nests from large fragments were located in a single 150-ha fragment (Hemlock Hill), while four were in a 152-ha fragment (Berlin). We sampled one territory each in two other large fragments; to assess the validity of including these two samples in our analysis, we tested their similarity to the nests sampled in the Hemlock Hill fragment (Sokal and Rohlf 1995). For one fragment, three of four feeding variables (deliveries/h/nestling, percentage of prey >20 mm, male deliveries/h/nestling, but not female deliveries/h/nestling) fit the distribution of the Hemlock Hill fragment. For the other fragment all four variables fit the distribution. Similarly, of the three arthropod sampling variables, one fragment fit the Hemlock Hill distribution for mean arthropod size and median arthropod size, but not total arthropod abundance, while the other fragment fit the distribution for all three variables. This suggests that the large fragments that were sampled using only one nest were not outliers for the majority of measured variables.

We used the Shapiro-Wilk test to determine if data were normally distributed (Sokal and Rohlf 1995). If data were not normal after transformation, we used nonparametric tests. We used regression analysis to compare feeding behavior and arthropod sampling. If residuals were not normally distributed after transformation we used the nonparametric Spearman's rank correlation (Zar 1996). Reported values are means ± SD. Two-sample tests were one-tailed; in most cases, the directed prediction was large > small. We performed power analyses for statistically nonsignificant

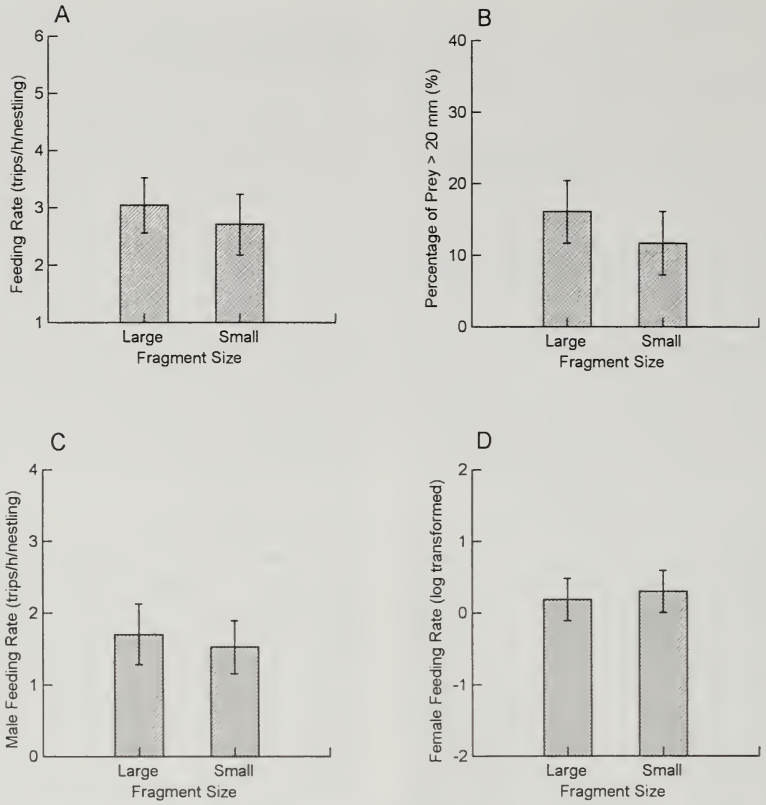

FIG. 1. Feeding behavior of Hooded Warblers nesting in large (.150 ha) and small (<4 ha) forest fragments in Crawford County, northwest Pennsylvania, 1999–2000. (A) Feeding rate per pair. (B) Percentage of large prey. (C) Male feeding rate. (D) Female feeding rate (log transformed). Values are means and 95% confidence interval. In all cases, there were no significant differences between fragment size classes.

results because accepting the null hypothesis carries the probability of Type II experimental error. Following procedures outlined in Steidl et al. (1997) power was tested for a hypothetical difference between means of 50% at $P = 0.05$, and effect size (d) is reported with the power value while 95% confidence intervals are shown in Fig. 1. This level of difference was chosen as biologically meaningful because other studies on the relationship between forest fragmentation and parental feeding reported differences between small and large fragments of ≥50% (Burke and Nol 1998, Zanette et al. 2000).

RESULTS

We did not detect a significant difference between large and small fragments in feeding rate per pair (Fig. 1; large = 3.04 ± 1.04, n = 21; small = 2.71 ± 0.87, n = 13; t = 0.96, P = 0.17, d = 1.42, power = 0.99), male feeding rate (large = 1.70 ± 0.89, n = 20; small = 1.52 ± 0.58, n = 12; t = 0.61, P = 0.27, d = 1.04, power = 0.87), or female feeding rate (log transformed; large = 0.18 ± 0.64, n = 21; small = 0.30 ± 0.46, n = 12; t = −0.54, P = 0.30, d = 0.9, power = 0.78). Males had higher overall feeding rates (trips/h/nestling) compared to their mates; however, the difference was not significant (paired t-test: t = 1.30, df = 30, P = 0.10). The feeding rate of males (Fig. 1C) and females (Fig. 1D) did not differ significantly between small and large fragments.

Pairs in large fragments likewise did not deliver a significantly greater percentage prey >20 mm (Fig 1; large = 16.02 ± 9.46, n = 21; small = 11.63 ± 7.18, n = 13]; t = 1.44, P = 0.08, d = 0.7, power = 0.62). During feeding trips, parents in both fragment size classes brought a wide variety of arthropod prey, including moths and their larvae, flies, beetles, and spiders.

The number of young fledged per nest was

TABLE 1. Arthropods sampled on Hooded Warbler breeding territories in large (>150 ha) and small (<4 ha) forest fragments, Crawford County, northwestern Pennsylvania, June 2000.

Variable	Large $n = 13$	Small $n = 12$	Test statistic	P
Total abundance	4.73	4.83	−0.61[a]	0.27[b]
Mean arthropod size	1.81	1.81	0.79[c]	0.22
Median arthropod size	1.65	1.87	1.24[c]	0.10

[a] *t*-test.
[b] d = 1.08, power = 0.83.
[c] S: Wilcoxon sign-rank test.

not significantly different between pairs in different fragment size classes (large = 2.57 ± 1.43, $n = 21$; small = 2.46 ± 1.27, $n = 13$; Wilcoxon sign-rank test: $S = 217.5$, $P = 0.72$) and partial brood loss attributed to starvation occurred in only one nest (in a 2.0-ha fragment). Regardless of fragment size, fledging success was not correlated with feeding rates per nestling (Spearman's rank correlation: $r_s = 0.202$, $n = 34$, $P = 0.25$). An insignificant difference in brood parasitism, measured by the number of cowbird eggs per nest, was found between fragment size classes (large = 0.48 ± 0.60, $n = 21$, small = 0.46 ± 0.52, $n = 13$, $S = 229$, $P = 0.97$).

Sweep netting indicated that none of the variables associated with arthropod size and abundance were significantly higher on territories in large fragments compared to those in small fragments (Table 1). However, in both small and large fragments arthropods >20 mm (size categories 4–5) were significantly less abundant than arthropods <20 mm (size categories 1–3) (*t*-test; small: $t = 9.46$, 11 df, $P < 0.0001$; large: $t = 6.27$, 12 df, $P < 0.0001$).

We examined if feeding rates per nestling were associated with arthropod abundance and size by comparing instances where both sweep netting and feeding behavior were sampled from the same territory ($n = 12$). Feeding rate per nestling was not significantly correlated with total abundance ($r^2 = 0.03$, $t = 0.58$, $P = 0.24$), or mean size class found on territories ($r^2 = 0.06$, $t = 0.81$, $P = 0.22$). The median prey size delivered to young was significantly larger than the median prey size sampled via sweep netting (two-tailed paired *t*-test: $t = -4.80$, 11 df, $P = 0.0003$).

DISCUSSION

This study is one of the first to investigate the relationship of fragmentation and parental feeding and food abundance. Our results indicate that Hooded Warblers breeding in small (<4 ha) fragments in northwestern Pennsylvania did not have a significantly lower feeding rate compared to pairs breeding in large (>150 ha) fragments over the years we studied. Furthermore, systematic arthropod sampling showed that small fragments did not have a significantly fewer or smaller arthropods. Our results are in contrast to those of Burke and Nol (1998) and Zanette et al. (2000). Burke and Nol (1998) found 10–36 times less leaf litter biomass on Ovenbird territories located in small fragments (>20 ha core area). Zanette et al. (2000) found that invertebrate biomass in small fragments was less than half of that found in large fragments. Power analysis demonstrates that our sample sizes were sufficient to detect differences of the magnitude found in these previous studies.

Relative to Ovenbirds and Eastern Yellow Robins, Hooded Warblers exhibit different space use patterns in forest strata. Ovenbirds forage primarily on the forest floor (Holmes and Robinson 1988) and Eastern Yellow Robins also capture invertebrates on the ground (Marchant 1986). The ground arthropods taken by these species can be susceptible to soil and leaf litter desiccation near forest edges (Matlack 1993). In contrast, Hooded Warblers are primarily gleaners (Evans Ogden and Stutchbury 1997) and increased light intensity near forest edges may have no effect on or actually increase the overall abundance of prey (Ferguson 2000, McGeoch and Gaston 2000). In the only other study to examine food supply of gleaning species, Nur et al. (1998) failed to find a relationship between Great Tit and Blue Tit feeding rates and fragment size.

Similar to the study of tits (Nur et al. 1998), we did not find higher feeding rates or larger prey items in large fragments. Despite this finding, it is possible that lower quality food (i.e., energy content or nutrition) is dependent upon fragment size. To investigate this idea, daily measurements of nestlings from hatching to fledging is needed. We know that parents did not compensate for less food by leaving small fragments in search of food because

radio-tracking studies in the same study site showed that Hooded Warbler females rarely left their territory fragment (Norris and Stutchbury 2002), and although males do leave fragments, these movements are primarily for extrapair copulation forays rather than foraging (Norris and Stutchbury 2001). However, parents may compensate for lower food availability with a higher feeding effort, thus spending more time provisioning young and less time in alternate activities. To investigate feeding effort an examination of adult activities while not feeding, and parental body condition and survivorship is needed.

Few studies have examined the relationship of forest fragmentation with arthropod abundance through direct arthropod sampling. Our sweep netting data indicated that none of the variables associated with arthropod size and abundance were significantly higher on territories in large fragments compared with those in small fragments. Our power analyses show that if differences do exist, they are modest and not of the magnitude detected by Burke and Nol (1998) and Zanette et al. (2000). Our findings are in accordance with a recent study by Sekercioglu et al. (2002) in which extensive sampling of invertebrate communities and avian diets revealed no important difference between large and small tropical fragments. The arthropod samples give an independent measure of whether food availability differs between fragment size classes. We know that Hooded Warblers forage extensively in the 2 m of understory where we sampled (Bent 1953; BJMS pers. obs.), and we found no significant difference in Hooded Warbler feeding rate, suggesting that food availability in general is not different.

In this study we sampled a wide variety of small fragments, but most of the pairs sampled in the large fragments came from a single forest, which limits the generality of our results (Hurlbert 1984). We minimized this bias by sampling pairs from throughout this fragment, which contained heterogeneous habitat types (primarily deciduous forest with heavy understory versus mixed coniferous/deciduous with light understory) and through a range of Hooded Warbler densities (see Tarof et al. 1998). Also, sampled nests included those in the center of the fragment and those near edges, and this fragment was of a size typical in this landscape. Furthermore, our small fragments were <4 ha, smaller than the forests sampled by Burke and Nol (1998) and Zanette and et al. (2000), suggesting we had a high probability of detecting edge effects if they were present.

Although edge effects are thought to cause a large reduction in food availability for forest birds (Burke and Nol 1998, Zanette 2000), our study, along with those of Nur et al. (1998) and Sekercioglu et al. (2002), suggest that this is not always the case. Clearly, to understand whether habitat selection and nesting success of forest birds in fragmented landscapes is influenced directly by food availability, more studies need to be conducted on species with various foraging behaviors.

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NEST SITE SELECTION BY FLORIDA SCRUB-JAYS IN NATURAL AND HUMAN-MODIFIED HABITATS

REED BOWMAN[1,2] AND GLEN E. WOOLFENDEN[1]

ABSTRACT.—Bird species having specialized nesting substrates could suffer reduced reproductive success in habitats modified by human activities where optimal nest sites may be in short supply. We examined nest sites of Florida Scrub-Jays (*Aphelocoma coerulescens*) in intact, natural oak scrub and in scrub islands embedded in a suburban matrix. Despite differences in vegetation structure between natural and suburban scrubs, scrub-jays used scrub oaks (*Quercus* spp.) as substrate for >80% of all nests in both habitats. Because of fire suppression, vegetation in suburban scrubs tended to be taller than in natural scrubs; however, in both habitats jays appeared to prefer shrubs slightly taller than those available. In both habitats, nest height increased with nest shrub height, but the relationship was stronger in suburbs. In suburbs, the height of nests relative to nest shrub height remained constant, whereas in natural scrub, nest height declined relative to nest shrub height. In both habitats, nests built near the top of shrubs were associated with the presence of *Smilax* spp., a perennial vine that provides dense foliage near the crown of oak shrubs. However, 68% of all nests in suburbs were associated with *Smilax*, whereas in natural scrub 9% of nest sites had *Smilax*. Few nest site characteristics, including habitat, were associated with nest failure, but nests built in oak shrubs were more successful than nests built in other vegetation. Suburban nests built near the top of relatively tall shrubs appeared to be more vulnerable to wind damage. *Received 30 July 2001, accepted 26 February 2002.*

Virtually all bird species are experiencing changes in their environment caused by humans. Measuring which anthropogenic changes might affect the survival of a species is a challenge for conservation biologists. The pace of anthropogenic changes to landscapes is so rapid that organisms may no longer be able to make optimal habitat selection decisions (Misenhelter and Rotenberry 2000, Remeš 2000), including nest site choices. Many bird species are highly selective in their choice of nest sites (Martin 1993), presumably because selection of appropriate nest sites is adaptive (Collias and Collias 1984). Certain species in the family Corvidae apparently select nest sites primarily to reduce nest predation (e.g., Hooded Crow, *Corvus corone cornix*; Loman 1979). Other corvids select sites to reduce negative effects of weather (e.g., Pinyon Jay, *Gymnorhinus cyanocephalus*; Balda and Bateman 1972). Nest site selection may result from a trade-off between opposing selective factors. For example, for some species in certain environments, the best sites to reduce predation may not be the best sites to reduce losses from inclement weather (e.g., Brown Jay, *Cyanocorax morio*; Lawton and Lawton 1980). Even within species, nest placement may vary to reflect geographic variation in climatic and biotic conditions (Schaefer 1976).

The Florida Scrub-Jay (*Aphelocoma coerulescens*) is a habitat specialist, requiring relatively open, low-growing (<2 m), oak-dominated scrub habitats. Scrub-jays typically nest in two species of oak shrubs (*Quercus geminata* and *Q. myrtifolia*), usually 1–2 m above the ground (Woolfenden 1974). Oak scrub embedded in a suburban matrix experiences reduced fire frequency, which increases the mean height of oaks and changes the oak species composition (Givens et al. 1984, Menges et al. 1993, Menges and Kohfeldt 1995). Suburban habitats also alter other ecological conditions, including the terrestrial predator community and degree of human disturbance of nesting birds (Erz 1966). Birds may nest higher in suburban habitats than in rural or natural habitats (Weber 1975, Savard and Falls 1981) because the vegetation tends to be taller, or because they are selecting sites that mitigate adverse environmental conditions endemic to suburbs. However, increasing nest height may increase the vulnerability to avian predators or susceptibility to destruction by strong winds (Graham 1988).

Here we compare nest site selection of Florida Scrub-Jays occupying natural, fire-maintained scrub to that in scrub islands embedded

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in a suburban matrix, and we examine the association of nest site characteristics with nest failure.

STUDY AREAS AND METHODS

The two study areas were 8 km apart at the southern end of the Lake Wales Ridge in Highlands County, south central Florida (27° 15′ N, 81° 25′ W). The natural scrub area is part of the 1,968-ha Archbold Biological Station (for area description, see Abrahamson et al. 1984) and has experienced a nearly natural fire regime for at least several decades (Woolfenden and Fitzpatrick 1984). Road construction and house building began in Placid Lake Estates, the suburban study area, in the late 1950s. Since then, the natural fire regime has been altered through fire suppression and habitat fragmentation. As a result, scrub in the suburban study area is patchily distributed and overgrown.

Florida Scrub-Jays nest from late February through June. At both study areas, all jays were color marked and the populations had been studied for 24 and 2 years, respectively. During 1993 we monitored every breeding attempt of each jay family in both study areas (n = 48, natural scrub; n = 58, suburban scrub). We found most nests during building or egg laying. For each nest found, we recorded the plant species, height of the plant, and height of the nest to the nearest 0.1 m (from the ground to the top of the nest rim). We also recorded the presence of *Smilax* spp., a perennial vine that provides dense foliage near the crown of oak shrubs. Once found, nests were visited every 2–3 days until fledging or failure. Nests that failed were inspected for evidence of the cause of failure. Successful nests were those that fledged ≥1 young.

To measure the relative availability of shrub species and their heights, we randomly selected 10 territories in natural scrub and 14 territories in suburban scrub. At each territory, we established a transect through the longest axis of the territory. At 1-m intervals, we recorded the species and height of the nearest stem of woody vegetation >0.3 m in height (Menges et al. 1993).

During 12–15 March 1993, a severe winter storm followed by unusually cold weather struck peninsular Florida (National Oceanic and Atmospheric Administration 1993). Archbold Biological Station experienced strong west winds (13 March: >50 kph for 12 h, maximum gusts of 100 kph) and abnormally low, freezing temperatures (14–15 March: minimum daily temperatures were 3° and −2°C, respectively, approximately 9°C below the long term monthly mean). Immediately prior to the storm, 13 jay pairs were incubating on nests in the natural scrub, and 27 pairs were incubating in the suburbs. We determined the fates of these 40 nests within two days after the storm.

We tested all data for normality using a Kolmogorov-Smirnov test. Because variances around nest height were not heterogenous in either habitat, we used the nonparametric Mann-Whitney rank sum test (Mosteller and Rourke 1973) for comparisons between habitats. We used likelihood ratio chi-square tests (Siegel 1956) to compare the relative frequency of plant species used as nest sites between habitats and also patterns of use versus availability both within and between habitats. Few nests were in plants other than oaks; therefore we pooled all non-oak nest sites to ensure that <20% of the cells in the contingency table had expected values <5. We compared the height of shrubs used for nesting between habitats using an independent unpaired t-test (Zar 1974). Pairwise comparisons were made using the Bonferroni pairwise procedure (Miller 1985).

We analyzed data only for nests in which ≥1 egg was laid. For jay groups with more than one nest during the 1993 season, we used mean nest height and mean nest shrub height for that group. We regressed the height of the nest shrub against both absolute and relative nest heights (proportional data were arcsine transformed) and then compared the slopes of these relationships between natural scrub and the suburbs using ANCOVA. To test for selection in the height of oak shrubs used for nesting, we assigned each shrub (those available and those used as nest sites) to a height class: 1–2 m, 2–3 m, 3–4 m, >4 m. We excluded shrubs <1 m because no jay nests occurred in such low shrubs. We pooled all oaks in the analysis and excluded other shrub species used less frequently by jays for nesting (n = 10 species). We used likelihood ratio chi-square tests to determine if the height distribution of all oak shrubs differed between study areas and if jays tended to select certain height classes within natural and suburban scrub. We tested for differences in the proportion of nests with *Smilax* using the Fisher exact test.

We used backwards stepwise logistic regression to determine nest site characteristics associated with nest failure. We compared all nests that fledged ≥1 young with those that failed, using habitat (natural or suburbs), shrub type (oak or not oak), nest height, the height of the nest shrub, the relative nest height (height of the nest/height of the nest shrub), and the presence of *Smilax* in the nest shrub as covariates. We performed a separate regression for nests built in oaks to determine if the species of oak chosen for nesting was associated with nest success. We compared nest height, nest shrub height, and the relative nest height of nests in the suburban area that did or did not survive the severe wind storm using ANOVA.

RESULTS

We found 103 nests in natural scrub and 119 nests in suburban scrub. In each habitat, four species of scrub oaks accounted for >80% of nest sites (natural scrub, 88%; suburbs, 82%; Table 1). Frequency of nests placed in oaks relative to all other species did not differ significantly between the two habitats (χ^2 = 1.1, df = 2, P = 0.29), but frequency of the various oak species differed (χ^2

TABLE 1. Plant availability versus use for nest sites of Florida Scrub-Jays nesting in two habitats during 1993, Highlands County, Florida. Values are percentages of plants in transects and plants used as nest sites.

Plant species	Natural scrub (n = 103)		Suburban scrub (n = 119)	
	Availability	Use	Availability	Use
Quercus geminata	25	32	39	46
Q. inopina	19	30	20	30
Q. myrtifolia	11	20	<1	3
Q. chapmanii	7	6	3	3
Persea humilis	<1	2	<1	8
Bumelia tenax	<1	0	1	2
Carya floridana	<1	2	1	3
Myrica cerifera	<1	0	<1	2
Ilex opaca	<1	3	<1	0
Ceratiola ericoides	<1	2	4	0
Lyonia fruticosa	4	1	6	1
Ilex glabra	1	1	0	0
Rubus spp.	0	0	<1	1
Serenoa repens	8	1	9	0
Ximenia americana	<1	0	1	1
Asimina obvata	1	0	<1	0
Lyonia ferruginea	1	0	3	0
Lyonia lucida	13	0	3	0
Pinus clausa	<1	0	<1	0
Pinus elliotti	<1	0	0	0
Sabal etonia	5	0	9	0

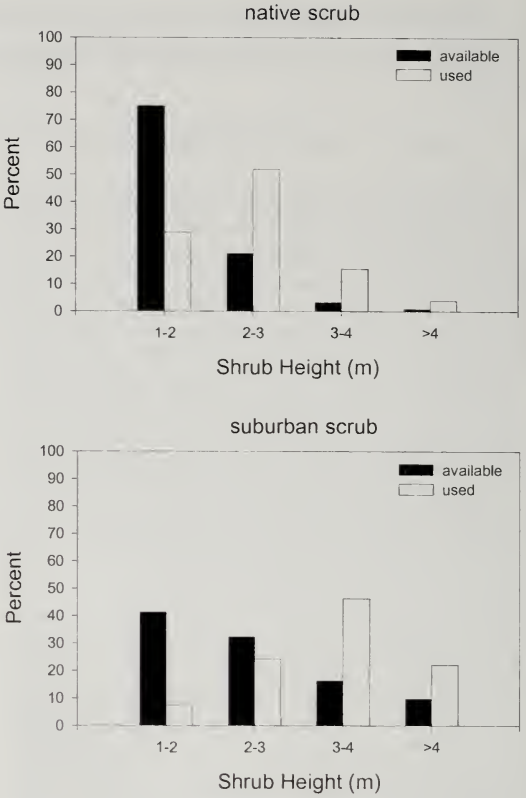

FIG. 1. Height distribution of available oak shrubs and those used by nesting Florida Scrub-Jays in native, undisturbed scrub and in a suburban matrix of disturbed scrub during 1993, Highlands County, Florida.

= 18.2, df = 3, P = 0.0004). In suburbs, scrub-jays used *Q. geminata* more and *Q. myrtifolia* less than did jays in natural scrub, reflecting differences in the availability of these two oak species between the two habitats. The relative use of *Q. inopina*, *Q. chapmanii*, and non-oak species as nest sites was similar between the two habitats.

Although we found no significant difference in the availability of oaks versus other shrubs that could be used for nesting by jays (χ^2 = 0.01, df = 1, P = 0.98), the distribution of individual oak species did differ between suburban and natural habitats (χ^2 = 13.0, df = 4, $P < 0.001$). *Q. geminata* was more abundant and *Q. myrtifolia* less abundant in suburban scrub than in natural scrub. In each habitat, oaks were selected over other shrub species for nesting (χ^2 = 9.1, df = 1, $P < 0.01$, natural scrub; χ^2 = 8.2, df = 1, $P < 0.01$, suburban scrub), but individual oak species tended to be used in proportion to their availability (χ^2 = 1.1, df = 1, $P > 0.50$, natural scrub; χ^2 = 1.4, df = 1, $P > 0.50$, suburban scrub; Table 1).

Shrubs used as nest sites were significantly taller in suburban scrub than in natural scrub (mean height: 3.4 m ± 0.07 SE versus 2.4 m ± 0.11 SE; t = 7.46, df = 1, $P < 0.001$) and this reflected the difference in the height of oak shrubs between the two habitats (χ^2 = 138.4, df = 3, $P < 0.001$; Fig. 1). In both habitats, jays preferred to nest in shrubs slightly taller than those available (χ^2 = 61.1, df = 3, $P < 0.001$, natural scrub; χ^2 = 52.1, df = 3, $P < 0.001$, suburban scrub; Fig. 1). In suburbs, most (68%) shrubs used for nesting also had *Smilax* growing at or near the crown. In contrast, *Smilax* occurred in only 9% of shrubs used for nesting by jays in natural scrub. Nests also were built significantly higher above the ground in suburban than in natural scrub (2.32 m ± 0.06 SE versus 1.15 m ± 0.09 SE, respectively; t = 22.5, df = 1,

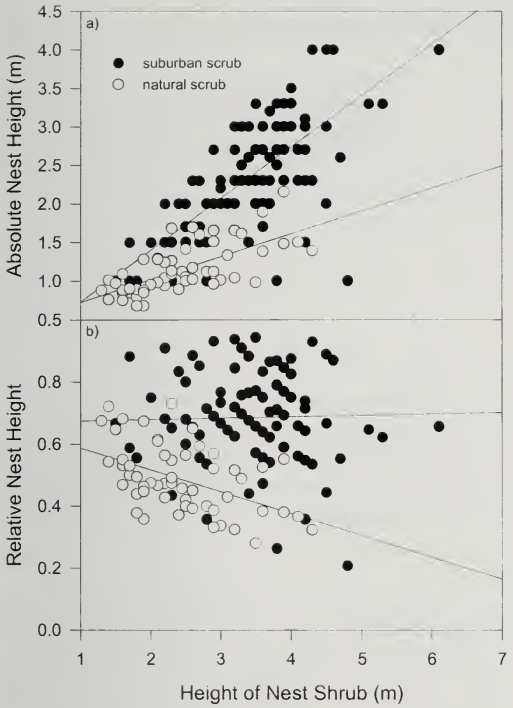

FIG. 2. Relationship between the height of the nest shrub and absolute and relative height (nest height/height of nest shrub) of Florida Scrub-Jay nests in native, undisturbed scrub and in a suburban matrix of disturbed scrub during 1993, Highlands County, Florida. The slope of the relationships of (a) absolute and (b) relative nest height to the height of the nest shrub are significantly different (ANCOVA, $F = 14.8$ and 7.2, $P < 0.001$ and $P = 0.008$, respectively) between the two habitats.

$P < 0.0001$). Only 2% of nests were built >2 m above ground in natural scrub ($n = 103$) compared to 76% in suburban scrub ($n = 119$). Relative nest height also was greater in suburban scrub than in natural scrub (mean 62.0% ± 0.01 SE, natural scrub; 76.8% ± 0.01 SE, suburban scrub; $t = 7.4$, df = 1, $P < 0.001$).

Nest height increased with the height of the nest shrub in both habitats, but more so in suburbs (Fig. 2a). In suburbs, relative nest height was constant regardless of the height of the nest shrub. In natural scrub, the relative nest height declined as the height of the nest shrub increased (Fig. 2b). Nests rarely were built in the lower third of a shrub in either habitat. However, because *Smilax* proliferates at the top of shrubs, the relative height of nests built in shrubs with *Smilax* was higher than those built in shrubs without this perennial vine in both habitats (Fig. 3).

Using logistic regression, we could not discriminate between successful and unsuccessful nests based on habitat, nest height, height of the nest shrub, relative nest height, and presence of *Smilax*; however, nests built in oaks tended to be more successful than those built in other vegetation (B = 5.01, Wald statistic = 4.12, df = 1, $P = 0.043$). For nests built in oaks, none of the above variables nor oak species was significantly associated with nest success. Although nest success did not differ significantly between natural scrub and suburbs (40.4% versus 47.8%, respectively), causes of nest failure differed ($\chi^2 = 6.67$, df = 2, $P = 0.036$) between the two habitats. While predation rates (0.65 versus 0.71) and abandonment rates (0.16 versus 0.25) were statistically similar between suburbs and natural scrub, weather-related losses were significantly higher in suburbs (0.19 versus 0.04).

Most weather-related losses in 1993 in suburbs occurred during the March storm, largely because of wind. Some nests literally were blown out of the nest shrub. Eggs, either broken or intact, were found below several nest sites. In suburbs, 11 of 27 nests active at the time of the storm failed. These failures included two nests that were deserted, probably because of heavy rains and cold temperatures as well as strong winds. Thus, conservatively, 33.3% of active nests (nine of 27) failed because of strong winds. In natural scrub, only two of 13 nests active during the storm failed, and of these only one could be attributed to wind. Thus, in natural scrub only 7.7% of active nests (one of 13) failed because of wind. These differences are marginally significant ($\chi^2 = 3.56$, df = 2, $P = 0.059$). Within the suburbs, nests that failed because of wind were built significantly closer ($F_{1,26} = 6.1$, $P < 0.05$) to the top of relatively tall shrubs (Table 2) and were more likely to be built in shrubs with *Smilax* ($\chi^2 = 6.4$, df = 1, $P = 0.018$) than those that survived the storm (63.6% versus 16.7%, respectively). Only nests built >2.0 m above the ground experienced wind damage.

DISCUSSION

Change in vegetation structure is known to influence intraspecific nest site selection at

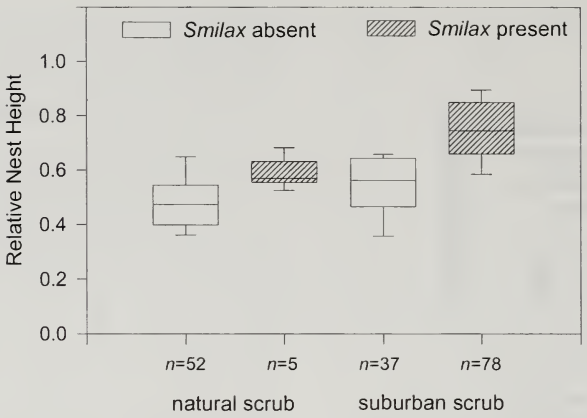

FIG. 3. Relationship between the presence or absence of *Smilax* and the relative height (nest height/height of nest shrub) of Florida Scrub-Jay nests in native, undisturbed scrub and in a suburban matrix of disturbed scrub during 1993, Highlands County, Florida. The box indicates the 25th and 75th percentile of relative nest heights, the solid bar within the box indicates the 50th percentile. The capped bars indicate the 10th and 90th percentiles.

broad geographic scales (Schaefer 1976), regional scales (Bekoff et al. 1987, Graham 1988) and local scales (Root 1967, Van Riper 1976). Suburbanization has many impacts on vegetation structure and composition (DeGraaf 1985), yet oak shrubs apparently suitable for Florida Scrub-Jay nesting remained abundant in our suburban area. As a result, scrub-jays used remarkably similar nest sites in the two habitats even though the relative availability of various shrub species of different heights differed. In both habitats, most nests were constructed in scrub oaks and nest height was proportional to the height of the shrub in which the nest was built. In the suburbs, jays used the four different oak species for nesting in different proportions than in natural scrub and their nests tended to be built higher above the ground. Both these differences are consistent with the structure and composition of available oak shrubs in suburbs, likely the result of fire exclusion. Oak species composition in scrub habitat changes in the absence of fire, with *Q. geminata* tending to increase in abundance with time since fire (Menges et al. 1993, Menges and Kohfeldt 1995). Because jays appear to select *Q. geminata* disproportionately for nesting in both suburbs and natural scrub (Woolfenden 1974), their increased use of this plant in fire-suppressed habitat was not surprising.

Most scrub oaks have numerous, stiff, divergent twigs which provide a solid nest foundation, protection, and concealment for the incubating jay. Relatively few other plant species common in natural scrub provide such nest sites. Therefore, in natural scrub, Florida Scrub-Jays rarely nest in vegetation other than oaks. The most frequent examples are rosemary (*Ceratiola ericoides*), crookedwood (*Lyonia ferrugenia*), fetterbush (*L. lucida*), scrub holly (*Ilex opaca*), young pines (*Pinus* spp.), and saw palmetto (*Serenoa repens*; Woolfenden 1974), which together constitute

TABLE 2. Proportion of Florida Scrub-Jay nests that survived a severe wind storm on 13 March 1993 in two different habitats, Highlands County, Florida. Values for nest height and relative nest height are means ± 1 SE.

	Proportion of nests		Nest height (m)		Relative nest height[a]	
Habitat	failed	survived	failed	survived	failed	survived
Natural scrub (n = 13)	0.08	0.92	1.2 ± 0.1	1.1 ± 0.2	0.47	0.49 ± 0.1
Suburban scrub (n = 27)	0.33	0.67	2.6 ± 0.5	1.8 ± 0.6	0.72 ± 0.1	0.59 ± 0.2

[a] Nest height/height of the nest shrub.

the densest shrubs in the Florida scrub other than oaks.

In suburban habitats, native birds may nest in exotic vegetation structurally similar to native vegetation, especially when native vegetation is rare or absent (Emlen 1974, Mills et al. 1989). In southwest Florida, where scrub-jays inhabit suburbs much older than our suburban study site, little (if any) native scrub vegetation remains and scrub-jays regularly nest in exotic shrubs (J. Thaxton pers. comm.). However, in our suburban study area where several species of exotic shrubs with growth characteristics similar to the oaks (e.g., *Viburnum*, *Ligustrum*, *Podocarpus*, *Citrus*) were common, jays almost always nested in the native species, especially oaks. Selection of oaks for nesting may be adaptive because nests built in oaks are more likely to succeed.

Suburban scrub-jays built their nest higher relative to the height of the nest shrub. The foliage of *Smilax* vines lies atop many shrubs, where it provides dense cover for bird nests. *Smilax* appears to be more abundant in suburban habitat, perhaps because of fire suppression or physical disturbance (Menges and Kohfeldt 1995). In both habitats, nests built near the tops of the nest shrubs were associated with *Smilax*. Suburban scrub-jays probably build their nests higher relative to the height of the shrub because *Smilax* is more common in this habitat.

Height alone may not be the most important criterion in nest site selection in suburban habitats (Graham 1988, but see Preston and Norris 1947, Weber 1975). In natural scrub, oak shrubs have relatively dense foliage from the crown to the base and jay nests are well concealed. With fire suppression, oak shrubs become trees and foliage tends to be denser near the crown and thinner toward the base. If jays seek to conceal their nests, they may build it near the densest foliage. Although we did not measure foliage density or nest concealment, nests associated with *Smilax* appear to be well concealed. Alternatively, suburban birds may nest higher in shrubs to avoid predators more common in suburbs (e.g., domestic cats, humans). However, in an urban population of American Robins (*Turdus migratorius*), habitat structure, measured largely by foliage volume, was the main determinant of nest height (Savard and Falls 1981).

Predation is the major cause of nest failure in scrub-jays (Woolfenden and Fitzpatrick 1984, Schaub et al. 1992) and jays probably select sites to minimize the probability of detection by these predators. Suburban scrub-jays likely perceive *Smilax*-crowned oak shrubs as suitable nest sites. Because none of the nest site characteristics, other than the use of oaks for nesting, could be associated with nest success, it appears that the stereotypical nest sites selected in both habitats were equally effective at deterring predation. Oak shrubs appear to provide the best nest sites for Florida Scrub-Jays, regardless of whether they occur in natural fire-maintained scrub or in fire-suppressed suburban scrub.

Perhaps surprisingly, habitat itself was not associated with nest success. In a separate analysis, we found no differences in success (defined as the probability of fledging ≥ 1 young) between jay nests in our suburban and natural scrub study areas over 8 years (Bowman and Woolfenden 2001). However, differences in the timing of nesting failure between the two habitats suggest that the two predator communities differ. Indeed, predator communities commonly differ between suburban and natural habitats (Tomialojc 1970, Churcher and Lawton 1987; A. L. Fleischer and RB unpubl. data), even though nest success of some suburban birds often is equal to that of birds in more natural settings (Gutherie 1974, Gering and Blair 1999, Bowman and Woolfenden 2001, but see Emlen 1974, Beissinger and Osborne 1982, Tweit and Tweit 1986, Mills et al. 1989). These patterns suggest that suburban birds may select nest sites that are appropriate to the local predator community.

Causes of nest failure other than predation are rare in scrub-jays. Wind accounts for very few failures ($<1\%$ over 10 years; Woolfenden and Fitzpatrick 1984), so nest site selection probably has little to do with ameliorating the effects of wind. In natural scrub, nests well concealed from predators also are likely sheltered and stable, and thus likely little affected by strong wind. In suburbs, nest sites that afford effective concealment from predators may be less sheltered and stable, located near the tops of relatively tall shrubs, and thus, may be more vulnerable to wind, as seen in our study area in 1993. In suburbs, predation and weather may be opposing potential selec-

tive factors. Storms of the magnitude of the one causing wind-related nest failure in this study are relatively rare and may not be a sufficient selective pressure to offset predation as the driving force for nest site selection. However, as habitats are rapidly altered by humans, behaviors such as nest site selection, that have evolved and are successful in native habitats, may become increasingly maladaptive in anthropogenic landscapes (Misenhelter and Rotenberry 2000, Remeš 2000).

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Conspecific Egg Predation by Florida Scrub-Jays

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ABSTRACT.—We report an observation of egg predation by conspecifics in the Florida Scrub-Jay (*Aphelocoma coerulescens*) at Archbold Biological Station in Highlands County, Florida. This is the first confirmed account of intraspecific egg predation in this threatened and declining species. We observed a group of five jays harass an established breeding pair at their nest that contained four warm eggs. One female intruder alighted on the nest and carried off an egg in its beak. Other intruding females also were seen at the nest and presumably removed two more eggs. The following day, the nest was deserted and contained only one cold egg. We discuss potential reasons for such conspecific egg predation, focusing on resource limitation. We believe that further research in this area is essential for this species in which competition for resources (e.g., nesting habitat) intensifies as suitable habitat declines. *Received 25 September 2001, accepted 14 March 2002.*

Egg predation by conspecifics is seldom observed and its contribution to egg loss in birds has been studied in only a few species (e.g., Vehrencamp 1977, Mumme et al. 1983). Egg loss is particularly noteworthy in the Florida Scrub-Jay (*Aphelocoma coerulescens*), a threatened species endemic to the state. Currently, this cooperatively breeding corvid numbers approximately 4,000 breeding pairs (Woolfenden and Fitzpatrick 1996) and continues to decline (D. Zattau pers. comm.). At Archbold Biological Station it has a mean nest success rate (nests that produce at least one fledgling) of 49% with a yearly range of 29–79% (Woolfenden and Fitzpatrick 1996). However, during our study (2001) nest success was only 38% (S. Schoech unpubl. data). While predation of Florida Scrub-Jay nestlings by snakes, mammals, and birds has been documented (Schaub et al. 1992, Schoech 1999), we know little about the frequency of predation or the identity of predators. In this paper, we describe the predation of Florida Scrub-Jay eggs by conspecifics.

METHODS

We observed color-banded jays residing in the south tract of Archbold Biological Station in Highlands County, Florida (27° 10′ N, 81° 21′ W, elevation 38–68 m; Schoech et al. 1991). Jays in the northern part of the station (demography tract) also were color marked and have been studied by Woolfenden and colleagues since 1969 (Woolfenden and Fitzpatrick 1984). We monitored the south tract jays continuously throughout the nesting season from late February to early June, 2001. We searched for nests daily from 07:30–12:00 EST and were particularly attentive to the nesting activities of jays occupying territories adjacent to the southern boundary of the demography tract. Jays occupying one of these territories in the northwestern corner of the south tract had been supplemented with a high fat and low protein diet provided *ad libitum* in the form of custom-made pellets dispensed from a feeder placed in the center of that territory. Since its establishment in the latter half of January 2001, this feeder had attracted jays from the demography tract immediately to the north. Incursions into south tract territories by increasing numbers of jays from the demography tract were thought to be the result of a wildfire that burned 259 ha of the 2,080-ha main property of Archbold Biological Station. The fire burned in the center of the demography tract on 12 February 2001 before any resident jays had constructed nests. Many territories, including some bordering the south tract, were extensively burned. Under these unusual circumstances, we describe below a conflict between neighboring Florida Scrub-Jays.

RESULTS

On 19 April 2001 we searched for a nest in the northernmost territory of the south tract. A fire lane running east-west separated the south tract from the northern demography tract. We found a group of nonbreeding jays (hereafter, the northern group) consisting of four females and one male from the demography tract perched on the north side of the fire lane. The female breeder of this group had

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been paired with the 15-year-old male for approximately one week. They did not attempt to nest during the 2001 breeding season (the male would later disappear and the northern group disband by the end of January 2002).

We walked south of the fire lane after observing the breeding male and female of the northernmost territory of the south tract (hereafter, southern pair) and searched the vegetation for this pair's first nest of the season. We followed the female for approximately 15 min; during this time her mate disappeared. The southern female soon started scolding when jays from the northern group entered the territory and approached to within 20 m of her. At 08:25 we found the nest of the southern pair, which contained four warm eggs, while the southern female was ≤3 m from the nest scolding us. She flew from branch to branch while head-bobbing, a movement expressed during territorial encounters, and vocalizing with both warning calls and hiccup calls, the latter a female-specific territorial vocalization (Woolfenden and Fitzpatrick 1984). As we moved away to mark the location of the nest, the northern group of jays moved to within 10 m of the nest. Several of the intruding females exchanged scolding vocalizations with the southern female, who head-bobbed continuously and hiccupped. The southern female chased one of the intruding females from the vicinity of her nest, but while she was gone, one of the unpaired northern females landed on the nest and looked inside. The southern female returned to her nest, driving the northern female away before returning to the nest to incubate the eggs. After ≤5 s, the southern female again left her nest to chase off another intruding female. Again, the southern female returned to incubate her eggs, and again chased off another bird. This time, in the absence of the southern female, the paired northern female landed on the nest and looked inside. She reached into the nest cup and departed with an egg secured in the tip of her bill. The unpaired northern female returned to the edge of the nest and also looked inside. However, at that time the southern female returned to her nest and drove the intruder away, after which she inspected the contents of her nest for several seconds. She left the nest once more to drive the northern group of jays out of her territory. The entire interaction lasted about 5 min.

After the predation event, the southern male returned. All intruding jays remained north of the east-west fire lane while the southern pair perched on the south side of the fire lane from where they watched the northern jays and occasionally head-bobbed. The southern female hiccupped several more times, but otherwise her vocalizations and those of the northern group ceased. At 08:45 we left the area.

SJR checked the nest again at 16:30 on the same day and only one egg remained. The following day the one cold egg remained when the nest was visited at 15:05, but no jays were observed in the area; the pair had abandoned the nest. Subsequently, the southern pair built a second nest and the female laid one egg, but this was found cold and abandoned on 11 May 2001. The southern pair subsequently bred during 2002.

DISCUSSION

Nonbreeding Florida Scrub-Jays are suspected of removing eggs from nests of conspecifics, based upon a single observation of a bird with a bill moistened perhaps from consumption of a conspecific's egg (Woolfenden 1973). Here, we directly observed one of a group of nonbreeders from a neighboring territory intrude into a breeding territory and take an egg from a nest of conspecifics. We assume that two more eggs from the nest were taken in the same way in our absence. Whether this form of egg loss contributes significantly to nest failure rates has yet to be determined.

We can only speculate on why the eggs were removed. The eggs may have been consumed. During the breeding season we observed members of the northern group and of the southern breeding pair at the feeder in the northwestern corner of the south tract, suggesting that there was foraging overlap between the two groups. With much of their foraging habitat burned by wildfire, the jays from the northern group may have been forced to forage farther afield, and the discovery of a conspecific's eggs may have presented them with an easy foraging opportunity. Florida Scrub-Jays readily take eggs and young of other species (Sprunt 1946). Similar behavior also has been reported in its congeners, the

Western Scrub-Jay (*A. californica*; Sprunt 1946, Carmen 1988) and the Mexican Jay (*A. ultramarina*; Brown 1994). Conspecific egg predation has been reported in the latter species (Trail et al. 1981).

Alternatively, destruction of eggs might be a mechanism of interference competition whereby conspecifics effectively space their nesting activities in the available habitat. For example, Quinn and Holroyd (1989) found that House Wrens (*Troglodytes aedon*) destroy the nest contents of Tree Swallows (*Tachycineta bicolor*) and of conspecifics in response to the limited availability of nest cavities. Since we report a case of possible intraspecific, as opposed to interspecific (e.g., Creighton and Porter 1974), competition, resource limitation might be even more intense under the conditions described above.

We observed the paired northern female removing the first egg, but other females may have removed two of the remaining eggs. No females of the northern group bred successfully during 2001 and most were unpaired. Only they, and not the male, approached the nest of the breeding pair while we watched. By removing the eggs, perhaps the unpaired females would improve their chances of acquiring a different type of resource: a mate. This argument also might apply to the paired northern female, given the advanced age of her mate. In some species, infanticide by male birds facilitates the acquisition of a new breeding territory (Robertson and Stutchbury 1988), a new mate (Kermott et al. 1991), or both. Egg destruction by female conspecifics is common in Bronze-winged Jacanas (*Metopidius indicus*; Butchart 2000) and results from the polyandrous mating system that creates a large population of unpaired females who challenge resident females for access to mates and territories. While Florida Scrub-Jays are socially and genetically monogamous and maintain strong pair bonds (Woolfenden and Fitzpatrick 1996, Quinn et al. 1999), divorce has been reported (Woolfenden and Fitzpatrick 1996). In this study, egg removal almost certainly caused the nest abandonment by the breeding pair, which perhaps could have led to the weakening of the pair bond and ultimately the liberation of the southern male and his breeding territory. However, this scenario is unlikely in our study area given the low annual divorce rate of 6% (Marzluff et al. 1996).

Whatever the underlying reasons for the observation described above, we cannot dismiss egg predation by conspecifics as being only a trivial contributor to nest failure in the Florida Scrub-Jay. In over 30 years of intensive study (Woolfenden and Fitzpatrick 1996), our account is the only direct observation of conspecific egg predation in the Florida Scrub-Jay. It is therefore tempting to consider this behavior rare in this species, but with continuing loss of suitable breeding habitat, such rare behaviors may become more common. Intraspecific egg predation in Florida Scrub-Jays warrants more detailed study.

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Effects of Fires on Foraging and Breeding Wading Birds in the Everglades

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ABSTRACT.—Nests, eggs, and chicks of nesting wading birds were unharmed by two fires in the Everglades. However, at least 50 adult White Ibises (*Eudocimus albus*) foraging away from the breeding colonies were killed during one fire. These results are counter-intuitive given that well-flighted adult birds seem more capable of escaping a fire than immobile nests or eggs. Nests probably were unharmed because of their location in wet willow (*Salix carolina*) and buttonbush (*Cephalanthus occidentalis*) islands. The adult birds foraging in a small cattail (*Typha angustifolia*) stand may have been trapped by flames in surrounding tall sawgrass (*Cladium jamaicense*) or debilitated by smoke inhalation. These observations provide insight into the direct effects of fire on wading bird breeding colonies and individual survival. *Received 27 June 2001, accepted 11 March 2002.*

Many studies have documented relationships among habitat, fire, and avian abundance (Howard et al. 1959, Vogl 1973, VantHul et al. 1997, Reynolds and Krausman 1998). However, the direct effects of fire on bird survival are rarely reported (Bigham et al. 1964, William and Stasiak 1979). Birds directly affected by fire usually are ground nesters whose eggs or chicks are vulnerable to ground fires (William and Stasiak 1979) or waterfowl that are flightless during wing molt (Hohman et al. 1992). Flighted, adult birds seem well equipped to escape fire and smoke. Here we report on the effects of fires on large breeding colonies of wading birds in the Ev-

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erglades and on the fire-related death of approximately 50 adult White Ibises (*Eudocimus albus*) found away from colonies.

We studied wading birds in northern Water Conservation Area 3A (WCA 3A) of the central Everglades ecosystem from January 1994 to July 1999. This area is a seasonally inundated grassland dominated by extensive stands of sawgrass (*Cladium jamaicense*) and cattail (*Typha angustifolia*). The flat, open landscape is occasionally broken by cypress heads and tree islands. Lower elevation islands are vegetated with willow (*Salix caroliniana*) and buttonbush (*Cephalanthus occidentalis*), cypress (*Taxodium* spp.), or introduced melaleuca trees (*Melaleuca quinquinerva*). A mix of tropical hardwoods is found on islands of higher elevation (Craighead 1971, Gunderson 1994).

Effects of fire on wading bird breeding colonies.—On 2 May 1994, we saw lightning start a ground fire north of Alligator Alley (Interstate Highway 75) and immediately west of Florida St. Rt. 27 in northeastern WCA 3A. This fire burned more than 2,833 ha during one week. The burned area consisted of contiguous stands of sawgrass and cattail, with widely dispersed tree islands. The study island is large (about 2 km greatest dimension), dominated by willow and buttonbush, and embedded in a matrix of cattail and sawgrass. This tree island ("Alley North") is the site of one of the largest wading bird colonies in the Water Conservation Areas (26° 11′ N; 80° 31′ W). At the time of the 1994 fire, the colony contained approximately 2,100 nests of wading birds (including White Ibises, Glossy Ibises (*Plegadis falcinellus*), Black-crowned Night Herons (*Nycticorax nycticorax*), Great Egrets (*Ardea alba*), Great Blue Herons (*A. herodias*), Roseate Spoonbills (*Ajaia ajaja*), Anhingas (*Anhinga anhinga*), Snowy Egrets (*Egretta thula*), Tri-colored Herons (*E. tricolor*), and Little Blue Herons (*E. caerulea*). On 8 May, we found that most of the grassy vegetation surrounding the colony was burned, although the lower stems and roots of grasses had been protected by shallow (about 2–10 cm) surface water. The shrubby vegetation within the colony showed no evidence of fire, even though the grassland vegetation on the immediate borders obviously had burned. Walking through the colony, we found no evidence of nest abandonment or of dead or moribund chicks of any species, despite the thick smoke that drifted into the colony during the fire.

On 16 April 1999, a larger fire, apparently of anthropogenic origin, began in the same area. The fire burned 70,010 ha north of Alligator Alley before ending on 30 April. During 1999, the Alley North colony contained approximately 8,000 nests of the same species that used the colony during 1994. As in 1994, the sawgrass and cattail surrounding the Alley North colony was burned to the ground, but the roots were protected by 2–5 cm of water or saturated soil. The vegetation within the colony did not burn. The 1999 fires also burned around the Mud Canal colony (26° 00′ N, 80° 32′ W) south of Alligator Alley, but the colony vegetation and nesting birds similarly were unaffected.

We conclude from these examples that under moderately wet conditions (i.e., soil still moist or covered by some surface water) the vegetation in willow and buttonbush colonies is unlikely to burn, and that fire poses little risk under these conditions to wading bird nests in the Everglades. Unlike tree islands dominated by tropical hardwoods, the substrate of willow tree islands is either lower than or at the same level as the surrounding marsh. Therefore, the willow and buttonbush colonies are likely to be as wet or in some cases in deeper water than surrounding areas. Further, willow and buttonbush do not tend to accumulate dead, above-ground biomass and create a moist, poorly flammable humus (Craighead 1971). Willow and buttonbush, therefore, provide relatively little fuel to initiate or sustain fires, especially when water is at or close to the soil surface. Large wading bird colonies are located almost exclusively in willow and buttonbush tree islands in the central Everglades (90% of colonies in 1994; Frederick 1995). Although this preference for nesting in wet or deep water areas may arise primarily because of the nesting birds' need for a water barrier beneath or surrounding the colonies for protection from mammalian predators (Rodgers 1987, Frederick and Collopy 1989), we suggest that nesting in willow colonies also provides a degree of protection from fires in wetland environments.

Fire-related mortality away from colonies.—As part of a study of White Ibis repro-

ductive physiology, on 1 April 1999 we trapped and radio tagged a female White Ibis near the Alley North colony in northern WCA 3A. Subsequently, this bird was identified through her activities as a breeder in the colony. On 21 April, this bird's transmitter gave a mortality signal, located approximately 7.6 km northeast of the colony. Upon reaching the site on 24 April, we found the carcass of the marked bird as well as approximately 50 other dead adult White Ibises. We found the birds within a 15 × 15 m space in the northwest corner of a stand of dense cattail (75 × 50 m), with a few dead birds scattered up to 150 m from this concentration. The cattail was desiccated and brown, but not burned to the same extent as the surrounding sawgrass. All birds were found ventral side down. The carcasses were badly decomposed and the feathers were charred and blackened. We concluded from the vegetation and the condition of the birds that the fire had passed across the cattail area relatively quickly.

Direct effects of the fire seem to be a plausible explanation for the death of the birds. The birds may have been debilitated by smoke inhalation or trapped at the cattail island with dense, low smoke overhead from the burning surroundings. The birds may have gone to the cattail stand to take refuge from the fire. The ibises also may have been purposely foraging close to the fire line, in response to insects or other prey being driven by the smoke and flame (Smallwood et al. 1982). The birds may have been unable to fly because of low, thick smoke, which could happen with a rapid wind shift. Indeed, the concentration of birds in this relatively unburned area suggests strongly that they were seeking refuge from fire and smoke.

Previous work has shown that nests and eggs on the ground are most susceptible to fire (William and Stasiak 1979), with an assumption that flighted birds could easily escape fire. Our report suggests important exceptions to these general rules. First, we found apparent selection of the least flammable vegetation by nesting ciconiiform birds, as well as little damage to nests during a fire, even to those of ground-nesting species. Second, we found a group of dead adult birds whose death was most likely caused by fire, suggesting that even flighted adult birds may not always escape the effects of fire.

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Survey for Reticuloendotheliosis Viruses in Wild Populations of Greater and Lesser Prairie-Chickens

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ABSTRACT.—Reticuloendotheliosis (RE) is a viral disease documented from poultry, which has been found to cause mortality in captive Attwater's (*Tympanuchus cupido attwateri*) and Greater (*T. c. pinnatus*) prairie-chickens. We surveyed blood samples from 354 Greater Prairie-Chickens from seven states collected during 1998, 1999, and 2000, and from 184 Lesser Prairie-Chickens (*T. pallidicinctus*) from three states during 1999 and 2000, for the presence of RE virus proviral DNA using a polymerase chain reaction (PCR) test. All samples were negative for the presence of RE virus proviral DNA except for two samples collected from male Greater Prairie-Chickens taken in Oklahoma during 1998. This suggests that RE may not be a serious problem for most wild populations of prairie-chickens. Although our results were largely negative, because of the serious consequences of RE, the presence of the disease in wild populations of prairie-chickens should be carefully considered in any future relocation and reintroduction efforts. *Received 30 July 2001, accepted 26 April 2002.*

Reticuloendotheliosis (RE) is a disease of a number of avian species, including domestic chickens (*Gallus gallus*), ducks, quail, pheasants, and domestic turkeys (*Meleagris gallopavo*; Bagust 1993, Witter 1997). RE has been found to cause morbidity and mortality in captive Greater and Attwater's prairie-chickens (*Tympanuchus cupido pinnatus* and *T. c. attwateri*; Drew et al. 1998).

Populations of the two species of prairie-chicken, Greater Prairie-Chicken (including the Attwater's subspecies) and Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) have declined dramatically during recent years (Westemeier and Gough 1999). It is not clear in many cases why the declines have occurred. Because of the serious effects of RE on captive prairie-chickens (Drew et al. 1998), it is important to determine if RE is a potential cause for the declines of wild populations. As pointed out by Friend et al. (2001), the ability to evaluate the effects of disease on a free-ranging bird species is fraught with difficulties. However, to begin to address the issue of whether RE was present in the wild populations, we surveyed for the presence of the disease in prairie-chickens across their range using samples collected during 1998, 1999, and 2000.

METHODS

We followed generally accepted procedures (Gaunt et al. 1999) for handling animals and obtaining samples. We collected about 1 ml of blood from the ulnar or jugular veins into 2-ml heparinized vacuum tubes. Because samples were collected during the execution of several disparate projects, the methods of handling and storage were not uniform; we describe the differences below. However, all samples met the minimum criteria for collection and storage to allow detection of the RE virus proviral DNA using the polymerase chain reaction (PCR).

During 1998, 1999, and 2000 we collected blood samples from 354 Greater Prairie-Chickens (231 males and 123 females) in seven states (Table 1). The greater number of males sampled reflects the fact that most trapping occurred on leks, where males predominate. Samples were obtained from Greater Prairie-Chickens on ≥38 trap sites, although in some cases these locations were <1 km apart.

We collected samples from four of the states, Wisconsin, Minnesota, North Dakota, and Nebraska, during 1998 and 1999 (Table 1) between July and August each year. We kept the samples on ice until centrifuged. The cellular fraction of each sample was frozen

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TABLE 1. The number of samples collected from Greater and Lesser prairie-chickens, by state, year, and sex (M or F). The number of samples corresponds to the number of individual birds sampled except for Okahoma, where 120 Greater Prairie-Chickens and 95 Lesser Prairie-Chickens were sampled (34 birds were sampled twice) and New Mexico where 74 Lesser Prairie-Chickens were sampled, with five being sampled twice.

	Greater Prairie-Chicken						Lesser Prairie-Chicken			
	1998		1999		2000		1999		2000	
State	M	F	M	F	M	F	M	F	M	F
Wisconsin[a]	12	6	18	2						
Minnesota[b]			18	10						
North Dakota[c]			10	8						
Nebraska[d]	4	8								
Missouri[e]			31	2						
Kansas[f]			30	48			3			
Oklahoma[g]	14	11	73	26	21	2	42	3	37	20
New Mexico[h]							22	5	34	18
Total	30	25	180	96	21	2	67	8	71	38

[a] Adams, Marathon, Portage, and Wood counties.
[b] Clay, Norman, and Polk counties.
[c] Grand Forks County.
[d] Garfield, Loup, and Rock counties.
[e] Barton, Dade, Pettis, and St. Clair counties.
[f] Greenwood, Morton, Lyon, and Waubansee counties.
[g] Beaver, Ellis, Harper, and Osage counties.
[h] Roosevelt County.

at −18°C until August 1999, when they were shipped to the Texas Veterinary Medical Diagnostic Laboratory (TVMDL) for analysis.

We collected samples from the remaining three states, Kansas, Missouri, and Oklahoma, during 1998, 1999, and 2000 (Table 1). Although it is unlikely, a small number of samples taken in Missouri may have been from birds transplanted from Kansas in 1995. We collected samples twice 1–13 months apart from 27 individual Greater Prairie-Chickens in Oklahoma to determine seasonal changes in prevalence of the disease (if it were present).

We obtained most samples from March through May of each year, although some samples were collected throughout the year. The samples were frozen (−70°C or −18°C) whole in heparinized tubes, except for 17 samples from Oklahoma during 1998, which were kept refrigerated (4°C) for 3–4 months before being shipped to the TVMDL for analysis.

We collected samples from 184 Lesser Prairie-Chickens (138 males and 46 females) in Kansas, Oklahoma, and New Mexico at 17 trap sites. The samples were collected throughout 1999 and 2000 (Table 1), although the majority were obtained from March through May of each year. Except for 19 samples from New Mexico collected during 1999, all samples were frozen (−70°C or −18°C) whole in heparinized tubes ≤4 h of being collected and maintained frozen until shipped to the TVMDL. The 19 New Mexico samples were refrigerated for three months before shipment to the lab for analysis. As with Greater Prairie-Chickens, we collected samples twice at least one month apart from seven individual Lesser Prairie-Chickens in Oklahoma and five from New Mexico to explore seasonal changes in prevalence of the disease.

All samples were shipped on dry ice to the TVMDL for analysis during July of each year. They were tested for the presence of integrated proviral DNA of the viruses causing RE using PCR methods previously described (Aly et al. 1993, Davidson et al. 1995). The TVMDL personnel were experienced in use of this technique with prairie-chicken samples.

RESULTS

Of the 538 samples, only two were positive by PCR for RE virus proviral DNA. Both were from male Greater Prairie-Chickens sampled in Osage County, Oklahoma, during 1998. Because these two samples had been refrigerated, not frozen, they had degraded to the point where virus isolation (as opposed to detection of the integrated proviral DNA) could not be performed to verify the presence of the active virus.

DISCUSSION

The positive results on two Greater Prairie-Chickens in 1998 from Oklahoma add to the few reports of reticuloendotheliosis viruses in free-ranging galliforms (Ley et al. 1989, Hayes et al. 1992, Drew et al. 1998). Samples collected from an additional seven Lesser Prairie-Chickens in the Texas panhandle during 1997 and tested at the TVMDL also were negative for RE (M. J. Peterson pers. comm.). Given only two positives of more than 500 samples,

RE appears to be uncommon and may not to be a major threat to prairie-chicken populations.

The occurrence of two positive birds from 25 collected in Osage County, Oklahoma, in 1998, but no other positive birds from other areas or other years invites explanation. Among the possibilities, not mutually exclusive, are (1) the two positive results could be false positives; (2) the virus was present in prairie-chickens during 1998 but not in subsequent years; (3) the disease may enter the prairie-chicken population from a reservoir species, and suitable conditions, such as a high vector population, may not occur in all years; and (4) the disease may have been present but not detected due to the timing of sampling. Further data are needed to evaluate the likelihood of these possibilities. In addition, it could be useful to investigate whether individual prairie-chickens have antibodies to the RE viruses. The detection of antibodies may help to identify birds that have been exposed to the virus but carry proviral copies at numbers below threshold sensitivity of the PCR test, and may provide information about past exposure to the disease.

Although our survey demonstrated at best a low prevalence of RE, because of the potentially serious consequences of RE described in Drew et al. (1998), the possible presence of RE in the wild populations of prairie-chickens should be carefully considered in any future relocation and reintroduction efforts.

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Prevalence of *Trichomonas gallinae* in Nestling Cooper's Hawks among Three North American Populations

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ABSTRACT.—Trichomoniasis, a digestive tract disease of raptors caused by ingesting the protozoan *Trichomonas gallinae* of infected columbid prey, recently was reported to be common in and an important agent of mortality among urban nestling and fledgling Cooper's Hawks (*Accipiter cooperii*) in Arizona. However, the prevalence of *T. gallinae* in wild raptor populations is poorly documented. During 2000 we detected *T. gallinae* in only three (2.7%) among 110 nestling Cooper's Hawks at 48 nests in both urban and rural habitats in Wisconsin, North Dakota, and British Columbia. Mortality attributable to trichomoniasis among 5- to 22-month-old Cooper's Hawks was zero in the three combined study areas. Prevalence of infection by *T. gallinae* seems to vary greatly among nesting Cooper's Hawks across this raptor's continental breeding range. *Received 30 July 2001, accepted 25 March 2002.*

Boal et al. (1998) reported that trichomoniasis, as contracted from consuming columbid prey infected with *Trichomonas gallinae* (a flagellated protozoan), was an important source of mortality among nestling and fledgling Cooper's Hawks (*Accipiter cooperii*) at urban nests in Tucson, Arizona. Although mortality in raptors due to this upper digestive tract disease has long been recognized, its prevalence in wild raptor populations is still poorly documented (Boal et al. 1998). During 2000, we investigated the prevalence of *T. gallinae* in 110 nestling Cooper's Hawks at 48 nests in both urban and rural habitats in Wisconsin (43 nestlings), North Dakota (32), and British Columbia (35). Columbids are known prey items of Cooper's Hawks in these three areas (Bielefeldt et al. 1998, Peterson and Murphy 1992; RKM and ACS unpubl. data), as in many other parts of North America (Bielefeldt et al. 1992, Rosenfield and Bielefeldt 1993).

STUDY AREAS AND METHODS

We located seven urban and four rural nests in or near Stevens Point, Wisconsin (population 23,000; 44° 25′ N, 89° 30′ W), one urban and 14 rural nests in or near Minot, North Dakota (population 35,000; 48° 37′ N, 102° 27′ W), and 19 urban and three rural nests in and near Victoria, British Columbia (population 200,000; 48° 27′ N, 123° 21′ W). For descriptions of study areas see Rosenfield et al. (1996), Murphy (1993), and Stewart et al. (1996).

We followed field and laboratory procedures described by Boal et al. (1998) to determine the presence or absence of *T. gallinae* in oral swabs from 1–4 nestlings aged 9–21 days (mean = 16 days) at each nest. Again following Boal et al. (1998), we re-examined all samples 4 days after initial testing for *T. gallinae* if it was not detected in the first test. If trichomonads were undetected after 4 days, we assumed them absent. However, if trichomonads were found in earlier screenings we tested the sample again at 7 days to reaffirm the presence of living *T. gallinae*. All samples that held living trichomonads on days 1 or 4 still held living *T. gallinae* on day 7.

All nestlings were marked with standard U.S. Fish and Wildlife Service aluminum leg bands, and in British Columbia with colored alpha-numerically coded bands as well.

RESULTS

We detected *T. gallinae* in only three nestlings (2.7%) at two nests (4.2%) among 110 nestlings (55 of each sex) at 48 nests (27 urban, 21 rural) on three widely dispersed North American study areas. All detections of *T. gallinae* came from urban nestlings (1 male, 2 females) in Victoria, British Columbia. Three infected young individually identified by color bands were still alive 5, 21, and 22 months after banding. Two infected young

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died, one from an automobile collision and the other from starvation due to a broken foot, 5 and 21 months, respectively, after banding. These deaths were not directly attributable to trichomoniasis. At least two infected nestlings were known to still be alive as breeding birds 1–2 years following marking. Among urban nestlings, mortality rate from trichomoniasis was zero in British Columbia (n = 30) and hence also zero among total urban nestlings (n = 54) and nonurban nestlings (n = 56) across the three study areas. Our results stand in marked contrast to the 41% mortality rate attributed to trichomoniasis among urban nestlings and fledglings (n = 157) in Arizona (Boal et al. 1998).

DISCUSSION

We examined the prevalence of infection by *T. gallinae* in nestling Cooper's Hawks in three widely separated populations at both urban and rural nest sites in Wisconsin, North Dakota, and British Columbia. These populations are not only spatially separate, but also morphologically separable (LJR, RNR, RKM, ACS and M. A. Bozek unpubl. data). Prevalence of nestling infection on our study sites was markedly lower than that reported by Boal et al. (1998) for both urban nest sites (5.6% versus 85%) and rural nest sites (0% versus 9%). Prevalence of infection by *T. gallinae* seems to vary greatly among nesting Cooper's Hawks in urban and probably rural habitats across its continental breeding range.

Boal et al. (1998) reported that trichomoniasis was an important agent of mortality among nestling and fledgling Cooper's Hawks in a population heavily infected with *T. gallinae* in Arizona. Because prevalence of infection by *T. gallinae* was very low in nestling Cooper's Hawks in our study areas during 2000, trichomoniasis was not a significant mortality factor. Boal et al. (1998) attributed the high prevalence of infection and consequent mortality in their study to the large proportion (83%) of columbids in diets of Cooper's Hawks at urban nest sites in Arizona. We know that nesting Cooper's Hawks prey on columbids on all three of our study areas. We do not know the proportion of columbids in nestling diets on these areas during 2000, but we do know that the proportion of doves in nestling diets on the Wisconsin and British Columbia study areas (about 5–8%) in past years (RNR, JB, and ACS unpubl. data) was much lower than the 83% reported by Boal et al. (1998). We do not know the dietary proportions of columbids that might result in high rates of infection by *T. gallinae* in nestling Cooper's Hawks. Although Hedlund (1998) reported the prevalence of infection by *T. gallinae* among three species of doves on the Tucson study area of Boal et al. (1998), the regional or temporal rates of infection in columbids themselves are unknown.

It is evident that infection by *T. gallinae* does not necessarily result in lethal trichomoniasis; none of the three infected nestlings died directly from trichomoniasis in our study and only half of the infected chicks became known deaths in Boal et al. (1998). The relative roles of infection rates in prey, the proportion of infected prey in diets, and the severity of infection in nestling hawks in causing mortality via trichomoniasis remain unknown.

ACKNOWLEDGMENTS

We thank the many undergraduate students at the Univ. of Wisconsin-Stevens Point for their field assistance. Funding was provided by the Personnel Development Committee and the Letters and Science Foundation at the Univ. of Wisconsin-Stevens Point, the Resources Inventory Branch of BC Environment, the Habitat Conservation Trust Fund, and the North Dakota, Wisconsin, and Great Lakes Falconers Associations.

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Ornithological Literature

Edited by Sara R. Morris

AVIAN INCUBATION: BEHAVIOUR, ENVIRONMENT, AND EVOLUTION. Edited by D. C. Deeming. Oxford Univ. Press, Oxford, United Kingdom. 2002: xiv + 421 pp., numerous black-and-white figures, sketches, and photographs. $85 (cloth).—This book is the most recent in the Oxford Ornithology Series, and like other texts in the series, *Avian incubation* provides a wonderful resource on an important part of the avian life cycle. The volume is the result of extensive literature review, takes advantage of the expertise of 27 authors, and provides a wonderful resource on the current state of knowledge about avian incubation.

The editor authored a number of the chapters in this book. He opens with "Importance and evolution of incubation in avian reproduction" that provides a context for the rest of the chapters, by interpreting the existing reviews that include incubation and stating that the goal of this text is "to bring together the wealth of information about incubation by birds in their natural environment." Furthermore, individual chapters, which are organized into five basic sections described below, not only summarize the current research, but also provide suggestions for future research on avian incubation.

The first section covers what the editor describes as fundamental aspects of avian reproduction. "Location, structure and function of incubation sites" covers a variety of topics related to nest site location, nest structure, and nest architecture. Egg morphology and composition, egg dimensions, and the egg shell are the subjects of "Functional characteristics of eggs." This section ends with "Embryonic development and utilisation of egg components," which covers patterns of development and changes to egg components.

The second section focuses on factors that affect the behavior of incubating birds and their embryos. The first chapter in this section, "Hormonal control of incubation behavior," includes sections on species and gender differences in prolactin levels and parental behavior, the role of steroid hormones and prolactin in initiating incubation, and behavioral effects on prolactin secretion. "Behaviour patterns during incubation" covers parental incubation including which parent incubates, other behaviors occurring during incubation, attentiveness during incubation, and the effects of attentiveness on clutches. This section ends with "Parent-embryo interactions," which includes a discussion of vocalizations, recognition, signaling of impending hatch, care solicitation, antiabandonment strategies, asynchronous hatching, and parental hatching assistance.

The maintenance of the incubation environment is the third section and includes chapters titled "The brood patch," "Maintenance of egg temperature," "Nest microclimate during incubation," "Patterns and significance of egg turning," and "Microbiology of natural incubation." "The brood patch" covers the location and positions of brood patches; the development of brood patches; differences among species; the hormonal control of brood patch development; mechanisms of action of the brood patch, both direct and indirect; and the functional activity of the brood patch. "Maintenance of egg temperature" includes a biophysical approach to egg temperature, both as a steady state and an unsteady state, and limitations to this biophysical approach. Temperature regulation of eggs, thermal considerations of incubating adults, nest humidity, nest gas composition, and egg turning are the subjects of "Nest microclimate during incubation." The process of egg turning, behavior patterns, egg position during incubation, turning frequency, reasons for egg turning during incubation, and evolutionary aspects of egg turning are covered in "Patterns and significance of egg turning." The final chapter of this section is "Microbiology of natural incubation," which covers fungal associations, bacterial communities, behavioral control of potential pathogens, and microbes on the egg surface.

The fourth section includes chapters on a

variety of species and species groups including "Underground nesting in megapodes," "Characteristics and constraints of incubation in hummingbirds," "Intermittent incubation: predictions and tests for time and heat allocations," "Incubation in extreme environments," and "Tactics of obligate brood parasites to secure suitable incubators." These chapters cover a variety of unusual aspects of incubation from the incubation mounds and techniques of the mound builders to tactics that nest parasites use to ensure host acceptance of eggs.

The final section of the book includes ecological and evolutionary aspects of incubation in the following chapters. "Ecological factors affecting initiation of incubation behavior" describes patterns in the onset of incubation and the significance of factors affecting the onset of incubation, including predation, temperature, and food availability. Crypsis, individual recognition of eggs and nests, filtration of solar radiation, eggshell strength, intraclutch variation in coloration, and specific colors of eggs are covered in "Adaptive significance of egg coloration." "Energetics of incubation" is a chapter that focuses on the energy constraints during incubation and the energetic costs of incubation in terrestrial birds and seabirds. The penultimate chapter in the book, "Incubation and the costs of reproduction," discusses why incubation might be costly and the distribution of incubation costs.

The editor ends with "Perspectives in avian incubation," which describes areas for future research on avian incubation. The discussion of the need for additional research and suggestions for areas of research are a major strength of this volume. An additional strength is in the references, which are extensive, appear to span both the early and the more recent work, and cover 86 pages.

I am sure that I will use this book often as a reference for my ornithology courses. Other professors and anyone interested in learning more about the nesting stage of birds will find this book a valuable addition to their library.—SARA R. MORRIS.

ANIMAL BEHAVIOR: AN EVOLUTIONARY APPROACH, seventh edition. By John Alcock. Sinauer Associates, Inc., Sunderland, Massachusetts. 2001: xiii + 543 pp., numerous color photographs and figures. $76.95 (hardbound).—This is the newest edition of what is arguably the best text on animal behavior. The major changes since the last edition, which was published four years ago, include a reduction of almost 100 pages of text, the revision of several chapters, and the addition of colored photographs, figures, and graphs. Although the entire text is about 15% smaller than the last edition, the references remain extensive and are decreased by only about 3%.

This version includes 15 chapters, 1 fewer than the previous edition. The chapters are "An evolutionary approach to animal behavior," "Proximate and ultimate causes of behavior: how and why birds sing," "The development of behavior: a focus on heredity," "The development of behavior: a focus on the environment," "The control of behavior: neural mechanisms," "The organization of behavior: neurons and hormones," "Adaptation and antipredator behavior," "The evolution of feeding behavior," "Choosing where to live," "The evolution of communication," "The evolution of reproductive behavior," "The evolution of mating systems," "The evolution of parental care," "The evolution of social behavior," and the "evolution of human behavior."

One of the most obvious improvements to this text is the addition of color to the photographs and figures throughout the text. The graphs have different colored lines, bars, or symbols for different sexes, treatments, or responses. These colored graphs are both easy to interpret and aesthetically pleasing. Students who are reading this volume as a text will find this change a substantial improvement to previous versions. Faculty may find the use of color photographs particularly beneficial for students who have limited experience with different taxa, specific species, and sexual dimorphism. This update alone makes the new edition a valuable addition to my personal library and an excellent resource for my students.

As a potential textbook, the use of bold terms for important vocabulary is an improve-

ment over the small capital letters used in the fifth edition, the most recent I had available. Likewise, minor changes in formatting and font will make the reading easier for many students. I greatly appreciate the continued use of numbered references in the text that reduce the space given to citations but maintain the importance of citing references appropriately. The summary at the end of each chapter and the discussion questions provide opportunities for students to review the main ideas and to practice using some of the new vocabulary and techniques they have learned. Finally, the suggested readings provide a great opportunity for students who are interested in a particular area to learn more about animal behavior. I highly recommend this book for any ornithologist, not simply those who are academics or interested in animal behavior.—SARA R. MORRIS.

ANIMAL ECOLOGY. By Charles Elton. Univ. of Chicago Press. 2001: lvi + 209 pp., 13 black-and-white photographs, and 13 black-and-white figures. $18.00 (paper).—This volume is a re-release of a work originally published in 1927, and released again in 1966. Students of science often lack a perspective on the history of their particular field, but this volume will help ecologists develop a better feel for the changes to ecology during the Twentieth Century.

The chapters from the original text are "Introduction," "The distribution of animal communities," "Ecological succession," "Environmental factors," "The animal community," "Parasites," "Time and animal communities," "The numbers of animals," "Variations in the numbers of animals," "Dispersal," "Ecological methods," "Ecology and evolution" and "Conclusion." The volume also includes the original editor's introduction, which was written in 1927 by Julian S. Huxley.

A new 28-page introduction, written by Matthew A. Leibold and J. Timothy Wooten, follows the editor's introduction and provides new prefatory material for each of the original chapters. The individual sections provide both the strengths and weaknesses of Elton's original text, places the topic into the context of modern ecology, and provides references for important works on the subject. The references for this introduction range from the late Nineteenth Century to the end of the Twentieth Century, providing historical context, research into emerging fields, and the current state of knowledge.

With the current emphasis on statistics and complex theoretical models, it was refreshing to read accounts of ecological processes that were more holistic in approach. Readers who are interested in learning more about the basic literature in ecology, the history of ecological studies, and a synthetic approach to ecology will find this an appealing read. I will certainly recommend it to my colleagues and students.—SARA R. MORRIS.

MIGRATION AND INTERNATIONAL CONSERVATION OF WADERS: RESEARCH AND CONSERVATION ON NORTH ASIAN, AFRICAN, AND EUROPEAN FLYWAYS. International Waders Studies No. 10. Edited by H. Hötker, E. Lebedeva, P. S. Tomkovich, J. Gromadzka, N. C. Davidson, J. Evans, D. A. Stroud, and R. B. West. International Wader Study Group, Thetford, Norfolk, United Kingdom. 1998: viii + 500 pp., numerous black-and-white tables, figures, and graphs. £35 plus postage and handling (paper).—This volume is the result of the 1992 international conference on "Migration and international conservation of waders," which was held in Odessa. As stated in the introduction, this work is "a unique compilation of long-term and short-term studies on waders in a little known part of the world, set in an international context." The volume is composed of 86 individual papers that range from single page abstracts to full length scientific articles. Although each article is in English, most originally were written in Russian, and Russian abstracts are included for most contributions. Despite being translated from their original language into English, the papers read clearly and are easy to follow. At the end of the volume is the translation of the Odessa Protocol into 13 additional languages. These translations are followed by two indices that are organized by scientific name and by common name of the species covered in these articles.

The volume is organized into six sections: "The Odessa Protocol," "Current approaches to wader conservation," "Flyway-scale migration research," "Wader research in arctic and subarctic regions," "Wader research in boreal, temperate, and steppe regions," and "Wader research in Africa." The section on arctic and subarctic regions is subdivided into two categories: (1) breeding and (2) migration and wintering, which is beneficial because almost half the papers belong to this general section. The six sections designated by the editors provide a means for conveniently organizing the papers, but could easily have been rearranged taxonomically, by scale of research, or by general type of research. Individual articles range from single-species routes and timing of migration, reproductive success and genetic structure, and daily activity patterns during the breeding season to large scale summaries of flyways, multispecies migration studies, and the importance of certain habitats for breeding waders. The wealth of information in this volume is extensive.

In the forward, the Ukrainian deputy minister indicates that by summarizing the current state of knowledge, this volume may help lead to conservation of habitats and international cooperation in the monitoring of avifauna. Most of the papers are descriptive, providing important information on the use of a variety of areas by waders. One of the early articles, "Towards a flyway conservation strategy for waders," provides a framework for assessing the current knowledge and developing conservation strategies based on available information. The appendix to this article is a table that summarizes the research and conservation activities that were part of the Odessa Protocol, and the number of proposals that already have been undertaken both by the Wader Study Group and by others is heartening. The group modeled much of their work on the Western Hemisphere Shorebird Reserve Network, which is further indication of international cooperation on the study of waders.

Biologists interested in migration, waders, or conservation will find this a valuable reference and an interesting read.—SARA R. MORRIS.

CHESAPEAKE WILDLIFE: STORIES OF SURVIVAL AND LOSS. By Pat Vojteck. Tidewater Publishers, Centreville, Maryland. 2001: xv + 152 pp., numerous color photographs. $34.95 (cloth).—This is better described as a coffee table book than a natural history book, but the author has taken care to provide interesting anecdotes and substantial life history attributes for a number of species. The result is a beautifully illustrated, interesting account of the wildlife of the mid-Atlantic region.

As the title implies, the author provides a history of the Chesapeake wildlife. The opening chapter provides early descriptions of the wildlife of the region, relying heavily on the writings of Captain John Smith. The next chapters describe a number of anthropogenic causes of wildlife mortality from the killing of "undesirable" species and the effects of agriculture, to the commercial hunting of wildlife for fashion or for food. Additional chapters address anthropogenic changes to the environment, including the degradation of water quality, the fragmentation of habitats, the introduction of exotic species, and the impact of DDT on wildlife in the mid-Twentieth Century. "An uphill battle" describes attempts to reverse human impacts on wildlife, particularly of endangered and threatened species. For example, the author includes an interesting account of the use of ultralight planes to teach Trumpeter Swans (*Cygnus buccinator*) to migrate back to the Chesapeake. She also recognizes the competing interests of different species in "Too much of a good thing," providing a clear, unbiased description of how some species, particularly white-tailed deer (*Odocoileus virginianus*) and Canada Geese (*Branta canadensis*), may have negative effects on other species of wildlife.

These chapters on the history and context of wildlife in the Chesapeake region are followed by descriptions of some of the particular species that are (or were) found in the region. Her section on deer and elk (*Cervis canadensis*) include discussions of changes in populations in the area as well as health concerns from the increase in the deer population, including the spread of Lyme disease. The species of wildlife that are described are generally widespread, making the relevance of this book extend well beyond the Chesapeake

area. For example, mammals include beaver (*Castor canadensis*), muskrat (*Ondatra zibethica*), river otter (*Lutra canadensis*), mink (*Mustela vision*), opossum (*Didelphis marsupialis*), raccoon (*Procyon lotor*), red fox (*Vulpes vulpes*), grey fox (*Urocyon cinereoargenteus*), bobcat (*Felis rufus*), coyote (*Canis latrans*), and eastern gray (*Sciurus carolinensis*) and red (*Tamiasciurus hudsonicus*) squirrels. Likewise, many species of birds covered are widespread, either in permanent range or as a result of migration patterns. Her discussion of waterfowl includes numerous aspects of life history including the difference between permanent and migrant populations, sexual dimorphism, mating behavior, and legislation that has affected many of these species. She also includes chapters on wading birds, raptors, seabirds, gulls and terns, backyard birds, and game birds. While the text is well researched and I did not find any glaring errors, it is limited by its nature. Nonetheless, the author has chosen information to include that provides a historical context, stories of destruction and loss to provide background for the importance of conservation, and some of the success stories to provide hope.

The value of this book truly is in the photography. The pictures are stunning and well chosen. She includes not only some of the most common and visible species, such as the Bald Eagle (*Haliaeetus leucocephalus*) and Brown Pelican (*Pelecanus occidentalis*), but also some of the species that would be overlooked by the casual observer, such as the Belted Kingfisher (*Ceryle alcyon*), the American Oystercatcher (*Haematopus palliatus*), and the American Bittern (*Botaurus lentiginosus*). Thus, these pictures may inspire a more thorough search by readers who may not be familiar with the species found in this area. While most ornithologists and conservation biologists will already know most of the information contained in this book, I doubt that this is the market for which it was intended. The interested backyard wildlife watcher or beginning naturalist is likely to find this book an interesting read that will provide added excitement to see some of the species covered. I certainly will consider this as a gift for some of my family members who are interested in learning more about their environment and just happen to be from the Chesapeake region.—SARA R. MORRIS.

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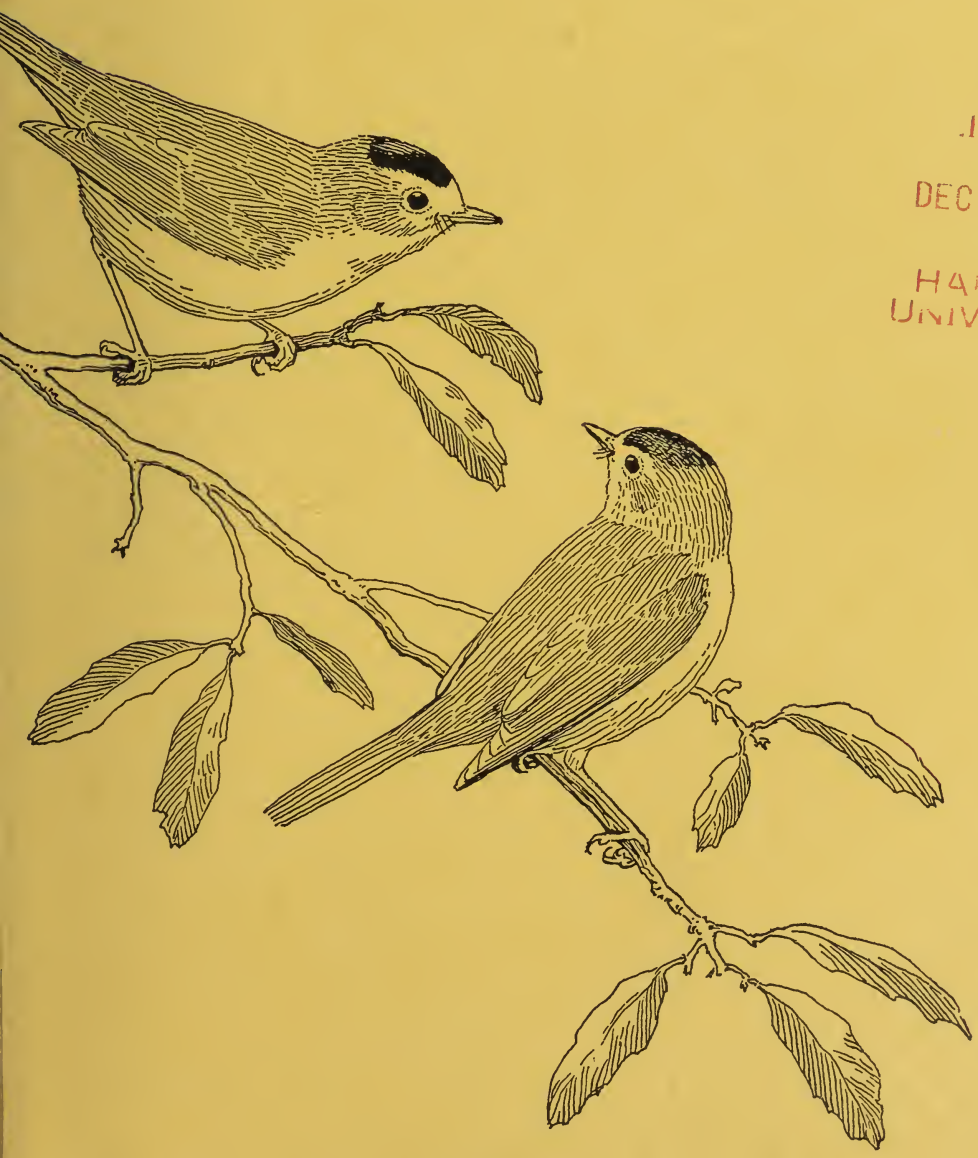

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THE MEXICAN SHEARTAIL (*DORICHA ELIZA*): MORPHOLOGY, BEHAVIOR, DISTRIBUTION, AND ENDANGERED STATUS

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ABSTRACT.—We reviewed morphological variation, taxonomic status, geographic distribution, ecology, and behavior of the poorly known hummingbird, the Mexican Sheartail (*Doricha eliza*), based on museum specimens and field studies. Although the broadly disjunct distribution of the species would suggest that two taxa are involved, morphological differences between the populations appear minor, not deserving of formal taxonomic recognition. Ecological differences between the two populations are stronger, however; modeled ecological niches are nearly nonoverlapping, and ontogenetic and behavioral differences may exist. We recommend that, given its extremely restricted distribution, the Veracruz population be considered critically endangered, whereas the Yucatan population be designated as having a restricted range and accorded near-threatened status. *Received 9 February 2001, accepted 22 July 2002.*

RESUMEN.—Se revisaron la variación morfológica, estatus taxonómico, distribución geográfica, ecología y conducta de un taxón muy poco conocido, el colibrí tijereta mexicano (*Doricha eliza*), en base en estudios de campo y en museo. A pesar de que la amplia disyunción en su distribución geográfica sugiere la existencia de dos taxones diferentes, la diferenciación morfológica es mínima y no amerita reconocimiento taxonómico formal. Sin embargo, las diferencias ecológicas entre las dos poblaciones son más marcadas, con nichos ecológicos modelados que casi no se sobrelapan, y diferencias ontogenéticas y de conducta pueden existir. En general, la población de Veracruz debe ser considerada en peligro de extinción, mientras que la población de Yucatán debe ser designada de distribución restringida y con un estatus de conservación de casi amenazada.

Although the endemic Mexican Sheartail (*Doricha eliza*) has been known for more than a century, little is known of this hummingbird's natural history. Its nest was only recently discovered and described, and the details of its geographic distribution are only now being understood (Ortiz-Pulido et al. 1998). Its generic placement is in question (e.g., Howell and Webb 1995, Johnsgard 1997, Ortiz-Pulido et al. 1998, American Ornithologists' Union 1998). The general picture, nevertheless, is one of a rare species with two disjunct populations, one in central Veracruz, and the other along the northern fringe of the Yucatan Peninsula (Howell and Webb 1995). Both populations are found in arid veg-

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FRONTISPIECE. Male and female Mexican Sheartail (*Doricha eliza*) of the Yucatan population. Watercolor painting by Marco Antonio Pineda.

etation, but the Yucatan population is more concentrated in the lowlands of coastal regions than that of the Veracruz population (Ortiz-Pulido et al. 1998).

Studies of other disjunct taxa generally have found clear sets of distinguishing characters, often at the level of species (Banks 1990, Peterson 1993, Garrido et al. 1999, Peterson and Navarro-Siguenza 2000). The two populations are thought by some to constitute recognizable taxonomic entities, in particular based on differences in the coloration of the collar (K. C. Parkes pers. comm.). The state of knowledge of these populations was so poor that the Veracruz population even was thought possibly extinct. Herein, we compare the two populations of *Doricha eliza* in terms of phenotypic, ecological, and behavioral variation. We also document the ecological and geographic distribution of the forms, leading to a reassessment of the conservation status of the species.

METHODS

To permit comparisons, we requested loans of specimens from scientific collections with holdings of the species (Appendix); in addition, MBR and GES collected a series of specimens of the Yucatan population, and deposited them at the Univ. of Kansas Natural History Museum (KUNHM) and the Museo de Zoología, Facultad de Ciencias, Univ. Autónoma de México (MZFC). We measured exposed culmen, wing length, and tail length (outermost and innermost rectrices) on each skin, and made comparisons of coloration in direct sunlight. Because measurements were not normally distributed, we used Mann-Whitney *U*-tests (Zar 1996) to test population differences for significance.

We made detailed observations of each disjunct population, recording food plants and describing behavior when possible. MBR and GES studied the Yucatan populations from 24 February to 1 March 1998 (18 km east of Dzilám de Brave; 21° 28′ N, 88° 34′ W; 0 m elevation), at the ecotone between mangrove and deciduous tropical scrub. ROP and RD carried out systematic surveys of the Veracruz population during June, August, October, and December, 1998, searching a rectangular area of about 3,200 km² (96° 58′ to 96° 25′ W, 19° 03′ to 19° 45′ N) in central Veracruz, based on records from the literature (American Ornithologists' Union 1998, Howell and Webb 1995, Ortiz-Pulido et al. 1998) and unpublished sight records (H. Goméz de Silva, S. Aguilar, and E. Ruelas pers. comm.). No reliable record known to us places the species outside of this zone. We chose a total of 20 sites within this area, based on elevation (five sites per 300 m of elevation, ranging 0–1,500 m), spaced by 10–20 km. During June 1998, we searched a 40 × 2,000 m transect at each site for hummingbirds. During August and October we searched another 20 transects focused within the more limited area within which the species had been encountered on the June searches. Methods for transect surveys followed established techniques (Emlen 1971, 1977).

We obtained additional distributional data from the *Atlas of the distribution of the birds of Mexico* data base (Peterson et al. 1998), based on the Mexican holdings of 43 museum collections in North America and Europe (listed in the Acknowledgments). We georeferenced all distributional data by direct inspection of maps and displays using ArcView (vers. 3.1) GIS software.

We developed ecological niche models for the two populations of Mexican Sheartail based on associations between point occurrence data and quantitative geographic coverages (including potential vegetation type; Rzedowski 1978), elevation, annual mean temperature, and annual mean precipitation (Comisión Nacional para el Uso y Conocimiento de la Biodiversidad, available at http://www.conabio.gob.mx/). Several approaches have been used to approximate species' ecological niches, including BIOCLIM (Nix 1986) and logistic multiple regression and generalized linear modeling (Austin et al. 1990). We employed the *Genetic Algorithm for Rule-set Prediction* (GARP), which includes both of the above methods and others in an iterative, artificial intelligence-based approach (Stockwell and Noble 1992, Stockwell 1999, Stockwell and Peters 1999). Individual algorithms were used to produce component "rules" in a broader rule-set, and hence portions of the landscape may be identified as inside or outside of the niche based on different algorithms. GARP therefore represents a superset of the other approaches, and should generally have greater predictive ability than any one of them. Extensive testing of GARP has indicated excellent predictive ability for species' geographic distributions (Peterson and Cohoon 1999; Peterson et al. 1999, 2000, 2001, 2002a, 2002b; Peterson 2001; Peterson and Vieglais 2001; Anderson et al. 2002; Stockwell and Peterson 2002a, 2002b). Ecological niche models were then projected back onto geography to predict potential distributional areas for each population.

RESULTS

We found no indication of differences in morphometric characters between the two populations. We examined 18 specimens (14 males, including 3 from Veracruz, and 4 females, 2 from Veracruz; Appendix). We found no significant differences in any morphometric character (all $P > 0.05$), nor did patterns of variation suggest consistent size or shape differences. Means for the four characters (adult males only, all measurements in mm) were for Veracruz ($n = 2$) and Yucatan ($n =$

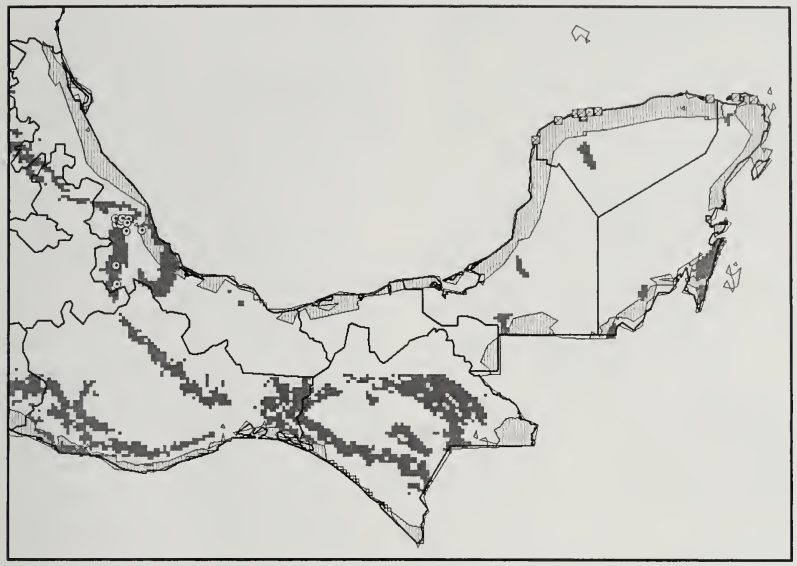

FIG. 1. Distribution of the Mexican Sheartail (*Doricha eliza*). Circles (with dots) indicate known occurrences of the Veracruz population, and squares (with x's) indicate occurrences of the Yucatan population. Potential distributions are shown in gray (Veracruz population) and vertical hatches (Yucatan population).

7), respectively: exposed culmen, 20.3 (range 19.6–21.0) versus 19.6 (19.0–20.8); wing length, 36 (35–37) versus 35.8 (34–37); outermost rectrices, 37 (36–38) versus 35.8 (35–38); and innermost rectrices, 24.5 (24–25) versus 24.4 (24–26).

Color characters also were closely similar in the two populations. At first inspection, adult Yucatan males appeared to differ from Veracruz males in having a white, rather than creamy, collar caudal to the gorget. Yucatan adult females also appeared to differ subtly in having underparts off-white, rather than buffy white, and Yucatan males appeared to have more bulbous, racquet-shaped tips to the tail than males from Veracruz. With more careful inspection, however, all color differences could be attributable to age variation, and differences in feather shape to feather wear. Hence, differences between the populations appear negligible, at least based on the small series of specimens presently available.

The ecological distribution of the two populations, however, is quite distinct. The Yucatan population is found exclusively in a narrow (ca 1 km) zone along the coast, particularly focused along the ecotone between mangroves and tropical deciduous forest. In contrast, the Veracruz population was far (25 km) from the coast, mainly in undisturbed arid vegetation (82% of observations). Indeed, about 30 years of field work by numerous observers at the Biological Station La Mancha nearby on the Veracruz coast have failed to produce a single credible record of the species (Ortiz-Pulido et al. 1995).

GARP models showed clearly the disjunct ecological distributions of the two populations, as well as only minimal corridors for movement of individuals (Fig. 1). The Yucatan population was modeled as inhabiting areas with 0–350 m elevation, precipitation broadly across all nine categories, and temperatures in only the three hottest categories, whereas the Veracruz population was modeled as inhabiting areas with 300–2,250 m elevation, precipitation in only the driest five categories, and temperatures in the three intermediate categories. Interpredictivity of the two ecological models, which would indicate identity of ecological niches (Peterson et al. 1999), is nil. Hence, the two forms of *Doricha eliza* are distinct in ecological dimensions.

Sex ratios in the two populations may differ, although the evidence is equivocal. The Yucatan population appears heavily biased to-

ward individuals with female-like plumage, perhaps an 8:1 ratio. During February 1998, we observed in an area of about 6.5 km^2 (18 km east of Dzilam de Brave, Yucatan) four adult (in definitive plumage) males and 30–35 female-plumaged birds. We observed no such bias in Veracruz, where searches revealed a 1:1 ratio for 22 individuals observed. This difference may suggest true differences in sex ratio or plumage sequences, but could easily result from different timing of field efforts for the two populations (i.e., the post-breeding observations in Yucatan may have detected more immatures than observations in Veracruz, which were later in the year).

During the study we observed known immatures in both populations. We collected two immatures in Yucatan. The first (KU 89385), collected on 26 February 1998, was a male with bursa of Fabricius, 12 colored feathers on the throat, and no grooves along the bill. The bill condition suggests that this individual was more than 9–12 months old (Ortiz-Crespo 1972). The second (KU 89386), collected on 26 February 1998, was a recently fledged (bill only 50% of adult length) male with no colored throat feathers that was being fed by a female-plumaged individual. We observed two immatures in Veracruz. The first, observed 7–8 November 1998, was a male about two months old, given that it was being fed by a female-plumaged individual. He remained perched on a twig for about 6 h, permitting careful observation. This male had colored throat feathers; presence of such feathers on such a young male might suggest that adult male plumage may be attained during the first year in the Veracruz population, reflecting differences in ontogenetic trajectories of the two populations. This evidence, however, is only circumstantial and more extensive information will be required before a credible conclusion may be drawn. The second immature, observed 21 March 1999, was a female-plumaged bird that was being fed by another female-plumaged individual.

We observed sheartails feeding at several plants. In Yucatan, sheartails fed primarily at viny, pink-flowered terrestrial plants of the genus *Ipomoea* (Convolvulaceae), and less frequently at small, terrestrial red flowers of the genus *Justicia* (Acanthaceae). In Veracruz, we saw sheartails forage on seven or eight plant species, most with red flowers: *Malvaviscus arboreus* (Malvaceae), *Hamelia patens* (Rubiaceae), *Salvia coccinea* and *S. purpurea* (Labiatae), *Triumfeta speciosa* (Tiliaceae), *Bouvardia ternifolia* (Rubiaceae), *Stenocereus griseus* (Cactaceae), and possibly *Solanum tridynamun* (Solanaceae).

We observed in Veracruz what appeared to be courtship behavior between members of a pair. For more than an hour we observed the pair chasing each other among the branches of shrubs and a tree, at times noisily. The male chased the female, and she would retreat to the center of a bush, about a meter above the ground. The male followed her, and began to display in front of her. The display consisted of holding his body in a horizontal position in the air in front of her, lifting his tail, and flaring out the red feathers of his gorget. All this time he hovered in the air, with head held still, and the body swaying left and right rapidly. During this display, he produced an intense *rrr-rrr-rrr-rrr* noise, which more or less coincided with the shifting of the body from side to side and lasted about 10 s. Howell and Webb (1995), apparently referring to the Yucatan population, reported that males in courtship move forward and backward in front of the perched female, with the body held vertically, climb to 30 m, and return to perch next to the female. We observed climbs and dives only once (May 2000) in the Veracruz population, and not clearly in a courtship context.

We observed a total of 22 individuals in Veracruz. The distribution of *Doricha eliza* in Veracruz is restricted to an elliptical area of about 40 × 20 km within the Barranca de Naolinco (Fig. 2). Population density in this region is only 0.033 individuals/ha (16 individuals on 480 ha of transects, with 6 individuals seen off transects). Although this density likely varies across the distributional area, extrapolating to the entire 800-km^2 distribution of the population yields an estimate for the entire Veracruz population of only about 2,500 individuals. The Barranca de Naolinco zone is relatively well conserved, given that much of the area is not suitable for most human activities; slopes are steep and the valley floor is covered with a heavy lava flow that prevents cultivation (ROP pers. obs.). Nevertheless, this zone is beginning to be used for grazing goats.

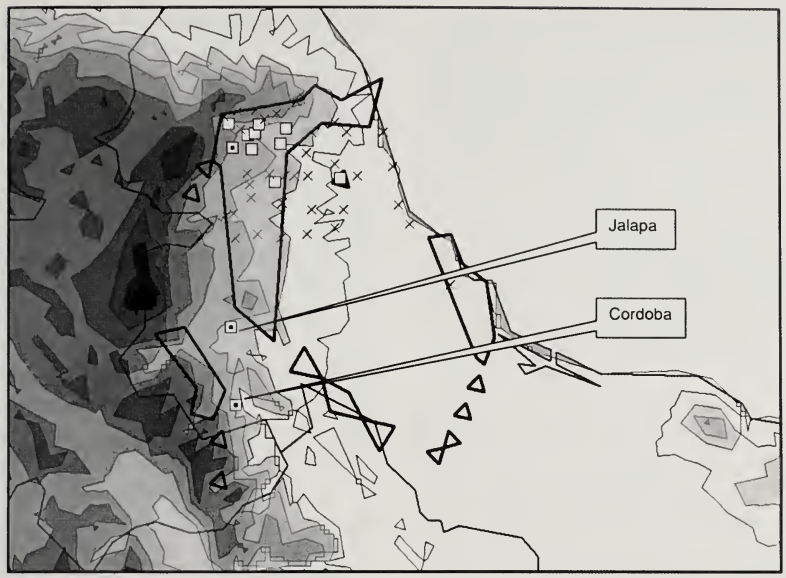

FIG. 2. Distribution of the Veracruz populations of the Mexican Sheartail (*Doricha eliza*). X's indicate sites surveyed without detecting the species, and squares indicate sites where the species was detected. Dotted squares indicate specimen localities, suggesting the imprecise nature of the earliest localities ("Jalapa" and "Cordoba"), but the correct descriptor of the more recent specimen ("5 mi N Jalapa"). Bold lines enclose areas predicted to be appropriate for the Veracruz population based on detailed ecological niche models of the occurrence points detected.

DISCUSSION

Population differentiation.—Our studies were necessarily based on few individuals, particularly in the case of the Veracruz population, the most recent specimen of which was collected in the 1930s (MLZ 22897). Nevertheless, our results show no evidence of differentiation among the two populations in the customary phenotypic dimensions: plumage coloration, size, and shape. However, we identify features of ecology that are distinct, and behavioral differences that are perhaps suggestive of population differentiation.

Geographic distribution.—The distributional points available for the two sheartail populations illustrate the broad geographic disjunction separating them, approximately 650 km (Fig. 1). Because no migratory behavior or movements are known for the genus, and given the broad ecological disjunctions, these populations almost certainly are genetically isolated, and have been for some time. The likely sister taxon of the Mexican Sheartail is the Slender Sheartail (*D. enicura*) found in scrubby montane forest in Chiapas and northern Central America. A possible sister genus to *Doricha* (genus *Calothorax*) occupies much of the arid Balsas Basin and Oaxaca Valley (*C. pulcher*), as well as the Chihuahuan Desert of northern Mexico (*C. lucifer*), but has no contact with any of the populations of *D. eliza*. It is notable that several important segments of dry deciduous tropical forest (e.g., the entire western coast of Mexico) remain uninhabited by any sheartail-type hummingbirds. Some evidence exists (R. Zusi pers. comm.) that the sister genus to *Doricha* might not be *Calothorax* but rather *Calliphlox*, which would complicate biogeographic interpretations considerably. It also would emphasize the need for detailed systematic discussion (e.g., Howell and Webb 1995).

Our surveys of the Veracruz population indicate that its geographic distribution is ≥50 km away from that reported by earlier authors (López-Portillo et al. 1993, Howell and Webb 1995, Johnsgard 1997). This difference of information clearly springs from a variety of problems, including basing records on unclear locality descriptors. For example, the type lo-

cality originally was described as "Pau du Taureau, entra la Vera Cruz et Xalapa" (= Paso del Toro, between Veracruz and Xalapa; American Ornithologists' Union 1998). Currently, at least five sites in central Veracruz are called Paso del Toro, causing considerable confusion as to its exact location. One of these sites, near the city of Veracruz, at <50 m of elevation, possibly could be the source of confusion. Another of the localities called Paso del Toro is Xalapa, fairly close to sites where the species has been observed (H. Goméz de Silva, S. Aguilar, E. Ruelas pers. comm.). However, the original Paso del Toro (and apparently the actual type locality) was abandoned in the Nineteenth Century owing to an outbreak of leprosy; the remains of this pueblo, located in the Barranca de Naolinco, still can be seen (ROP pers. obs.). Other early specimens were labeled with little precision ("Jalapa" or "Veracruz"); only with the 1939 C. C. Lamb specimen (MLZ 22897) does a locality coincide with the species current observed distribution. Our highest elevation record for a Veracruz sheartail was 1,390 m, and no clear records place it even slightly higher in the vicinity of the city of Xalapa (1,400–1,600 m).

Conservation.—The conservation status of the two sheartail populations differs: one population is vulnerable whereas the other appears critically endangered. Both have extremely restricted ranges, and would qualify as "endemic" under the range-based definitions (Bibby et al. 1992), although this phenomenon is better termed "restricted range" (Peterson and Watson 1998). The Yucatan population, however, occurs in many areas under no immediate threat, and is present in at least three protected areas (Biosphere Reserves Ría Lagartos and Río Celestún, Special Biosphere Reserve Bocas de Dzilám de Bravo). Although the population is vulnerable, we recommend not according any formal status designation of threat or endangerment, although rapid development of the northern Yucatan Peninsula for tourism could change this situation.

The Veracruz populations, however, are found only very locally in a limited sector of central Veracruz. Their geographic distribution is centered within one of the largest foci of habitat destruction in the country, and the dry deciduous forests that it inhabits are being rapidly modified for grazing, cane sugar cultivation, and other human activities. Central Veracruz has been a major focus of habitat destruction over the past several centuries, fragmenting the sheartail population's distribution from the onset. The distribution now centers on a single canyon, but the extreme rarity of specimens and reduced population suggest that the decline of the population may not result so much from present-day habitat fragmentation as from natural restriction of range. This phenomenon, however, certainly is exacerbated by ongoing habitat fragmentation. The recent introduction of goat grazing in the region poses a serious threat to the vegetation. For these reasons, we recommend that the Veracruz sheartail populations be considered critically endangered. Measures for their protection are urgently needed.

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APPENDIX

Specimens examined.—Mexico, Veracruz, Jalapa, three males, one female (ANSP 23450, 37949, 37953; BMUK uncat.); Veracruz, 5 mi

N Jalapa, 4450′, one female (MLZ 22897); Yucatan, 18 km E Dzilam de Bravo (type locality), three males (KUNHM 89383–5); 3.5 km S Progreso, two males (DMNH 18912, UMMZ 201853); Progreso, one male (LSUMZ 25123); Mérida (exact locality uncertain), one male (MLZ 25846); 3 km E Chicxulub Puerto, E of Progreso, four males, two females (DMNH 18907, 18908, 18909, 18910, 18911, 18913).

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FIRST DESCRIPTION OF THE NEST OF THE CHESTNUT-TAILED ANTBIRD

A. BENNETT HENNESSEY[1]

ABSTRACT.—Here I describe for the first time nests of the Chestnut-tailed Antbird (*Myrmeciza hemimelaena*) in Bolivia. I found two nests in the understory of tropical lowland and hill tropical forests. The nests, 25 and 28 cm above ground, were basally supported open cups with a curved *Geonoma* sp. palm leaf as the structural foundation, woven with pieces of brown stringy rootlets, dead leaves, and leaf exoskeletons. *Received 25 July 2001, accepted 26 March 2002.*

The Neotropical family Thamnophilidae (Sibley and Alquist 1990, Sibley and Monroe 1990) is large, yet relatively poorly known (Ridgely and Tudor 1994), and nests, eggs, and nestlings of most species are undescribed (Wilkinson and Smith 1997). Here I describe for the first time the nests, eggs, and nestlings of the Chestnut-tailed Antbird (*Myrmeciza hemimelaena*) from sites in eastern Bolivia. *M. hemimelaena* is a resident of humid forest undergrowth, predominantly in the Southern Amazonia and the lower Central Andes zoogeographic regions, with a less common occurrence in the southeastern region of Northern Amazonia (Stotz et al. 1996). *Myrmeciza* is a heterogeneous and probably polyphyletic genus, and *M. hemimelaena* belongs to a group of smaller, strongly patterned and usually more colorful species (Ridgely and Tudor 1994).

M. hemimelaena is one of the more common tropical forest understory antbirds in Bolivia (ABH pers. obs.). It often is the last remaining forest antbird species in the most southerly remnants of the Amazonian avifaunal community in Bolivia (ABH pers. obs.). Vocalizations and plumages of *M. hemimelaena* have been described (Meyer de Schauensee 1970, Willis 1985, Ridgely and Tudor 1994, Mayer 2000) and recorded vocalizations (songs, contact and alarm calls) have been archived by the author (MLNS 101829 and 101702, Macauley Library of Natural Sounds, Cornell Univ.); however its nest has not been described previously.

I found the first nest at 900 m (15° 06′ S, 67° 32′ W) in the Pilón Lajas Biosphere Reserve and Communal Lands on the northern slope of Serranía Beu (peak at 1,600 m), Provincia Franz Tamayo, Dept. La Paz. The vegetation of the area is hill tropical humid forest (Stotz et al. 1996). I found the second nest at 290 m (14° 33′ S, 67° 43′ W), in Madidi National Park, Provincia Franz Tamayo, Dept. La Paz, between the Tuichi and Hondo rivers. The area is mature, lower tropical humid forest between Serranía Bala (800 m) and Serranía Eslabón (2,000 m). I found both nests during bird surveys by unintentionally flushing the birds from their nests. Each female sat quietly on her nest until startled, then flew 4–5 m off and gave alarm calls.

Both nests were open cups basally supported by a curved *Geonoma* sp. palm leaf, which also served as the nest's structural foundation. They were attached at the side to one object, but supported from underneath. I found the first nest during incubation on 21 September 1998 and a female flushed once daily (11:00–14:00 EST) to 25 September. The nest originally had been beside the basal stalk of a tree fern, hidden underneath its lower frond. The stalk had been cut during trail maintenance, exposing the nest (Fig. 1). The nest (7.5 cm high, 12 cm in diameter; Fig. 2) was on a small ledge 25 cm above ground on a vertical bank. Below the nest was a disused hole 11 cm in diameter. The nest rested on debris and was attached by one side to forest litter and roots projecting from the earth. The inside had pieces of brown stringy rootlets and two leaf exoskeletons. The outside was mainly strips of palm leaf with dead leaves and some rootlets.

On 2 March 2001 I located the second nest (6 cm high, 10.5 cm in diameter), after flushing the female, exposing two nestlings. It was

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FIG. 1. Exposed nest of Chestnut-tailed Antbird (*Myrmeciza hemimelaena*) at Serranía Beu, Pilón Lajas Biosphere Reserve and Communal Lands on 23 September 1998. Photograph by A. B. Hennessey.

FIG. 2. Nest with two eggs of Chestnut-tailed Antbird (*Myrmeciza hemimelaena*) at Serranía Beu, Pilón Lajas Biosphere Reserve and Communal Lands on 23 September 1998. Photograph by A. B. Hennessey.

28 cm above ground on a discarded dead palm leaf that had fallen over a thin sapling (1.5 m high). Like the first nest, the nest was basally supported by a structural foundation of a single curved dead *Geonoma* sp. palm leaf, with small dead leaves and thin strips of palm leaf woven into a circle. The nest was attached to the sapling stalk with the same material.

The clutch and brood size for the first and second nests, respectively, were two. The eggs were pyriform to long-pyriform (2 cm long, 1.4 cm in diameter) cream-white, with lengthwise faint, thin, pink scrawls, concentrated toward the blunt end (Fig. 2). The nestlings were purplish blue, without down. They were inactive and had closed eyes.

The antbirds I observed created basally supported nests, but placed them above the ground. This possibly demonstrates the evolution of an ancestral ground-nesting trait in response to predation pressure. In future observations it will be important to note if the nests are above ground and basally supported by a palm leaf that functions as its structural foundation. Additional information on the nests of other species may aid our comprehension of the taxonomy and evolutionary history of this genus and the Thamnophilidae.

ACKNOWLEDGMENTS

I thank Vétérinaires Sans Frontières, financed by the British, Dutch, and Swiss governments, for supporting Pilón Lajas Biosphere Reserve biological research. I also thank the Living Landscapes Program of the Wildlife Conservation Society, financed by USAID/Global and WCS International through cooperative agreement LAG-A-00-99-00047-00. The opinions expressed are those of the author and do not necessarily reflect USAID criteria. I also thank the Protected Areas Service for permission to work within Madidi National Park. I especially thank S. Mayer, B. Whitney, G. Budney, The Macaulay Library of Natural Sounds, and BirdLife International for support and assistance.

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THE COURTSHIP DISPLAYS AND SOCIAL SYSTEM OF THE WHITE-RUFFED MANAKIN IN COSTA RICA

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ABSTRACT.—We studied the relationship between group and individual display in the courtship and social system of the White-ruffed Manakin (*Corapipo leucorrhoa altera*) in the Atlantic slope foothills of Costa Rica. Between 20 April and 28 May 1989, we searched for display logs and conducted 358 h of observations focused on four display logs. We found logs owned by a single resident male in which activity was continuous, as well as logs and areas where displays were occasional. Six of the eight logs found in the study area were arranged in two clusters separated by about 300 m, although we also found a solitary log 200 m from the nearest active display site. The resident male was at his display site 40.7–93.7% of the time, mostly alone. Residents were visited by other males mainly before 08:00 and less frequently by females later in the day. Residents continually gave advertisement calls during the day and performed several visual displays, including an elaborate *Flap-chee-wah* in which the male would fly steeply upward from the display log to land explosively at high speed a few seconds later, instantly jumping while turning in the air to land facing the original landing point. Two of these displays culminated in copulations. Other common displays were a slow undulating Butterfly flight and Throat-flagging in which males slowly moved their heads, exposing the fully erected, contrasting white throat feathers. Males performed the displays alone, in the company of other males, or in the presence of females. We conclude that *C. leucorrhoa* displays in dispersed leks as found by other authors for *C. gutturalis*. Each log is owned by a single individual and the visits by other males may have a social function related to the establishment of a dominance hierarchy. We found important similarities between the two species of *Corapipo* and also with the genus *Masius*, which supports the proposed close relation between the two groups. *Received 10 July 2001, accepted 12 March 2002.*

The family (or subfamily) Pipridae, the manakins, is a Neotropical group closely related to New World flycatchers and cotingas, and currently is considered to include 40 species in 10 genera (Prum 1990). The group, in which all studied species show polygyny and lek/arena display, is best known for its variety of elaborate and peculiar courtship rituals performed by the males, which in most cases have much more colorful plumages than do females (Snow 1963, Sick 1967, Prum 1990). In lek breeding systems, males do not establish any lasting pair bonds with females. They defend nonresource-based display territories, the aggregation of which is defined as a lek (Bradbury 1981). According to the size of individual courts and the number of males in an aggregation, several types of leks have been identified in manakins: concentrated leks with usually >5 males aggregated, holding individual territories 1–5 m in diameter; dispersed leks, formed by 2–7 males holding territories 10–40 m in diameter; and solitary leks in which males holding display territories 10–30 m in diameter are isolated from others (Prum 1994).

The White-ruffed Manakin (*Corapipo leucorrhoa*) inhabits lower and middle levels of dense wet forests from southeastern Honduras to northwestern Venezuela. The species comprises three subspecies that differ slightly in the extent of white in the throat and primary feather morphology: *C. l. leucorrhoa* (Sclater) from Venezuela and Colombia, *C. l. heterolecua* (Hellmayr) from Panama and southern Costa Rica, and *C. l. altera* (Hellmayr) from northern Costa Rica to Honduras, the subject of this study. Some authors consider *C. altera* from Central America and western Colombia to be a distinct species from *C. leucorrhoa* from eastern Colombia and Venezuela (Stiles and Skutch 1989, Wetmore 1972). Adult *C. leucorrhoa* males are glossy blue-black with a white throat patch; females and first year males are olive-green, usually with a grayish tint on the throat.

During their second year they are capable of mating (Aldrich and Bole 1937) and males have a distinct plumage, with a black mask and a partially white throat (Rosselli 1994). Females are heavier than males (12.5 g ± 0.19

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SE, $n = 30$, and 11.1 g ± 0.09 SE, $n = 87$, respectively; Rosselli 1994), a characteristic that has been linked to displays in *C. gutturalis* (Théry 1997). The species is highly frugivorous and in Costa Rica its reproductive season extends between March and June (Skutch 1967, Rosselli 1994). The displays of the *altera* and *heteroleuca* subspecies of the White-ruffed Manakin were described by Aldrich and Bole (1937), Slud (1964), Skutch (1967), and Rowlett (in Davis 1982). Displays take place on fallen mossy logs in the forest, and include slow undulating flights between perches and approaching the display log, hops on the display log, flight song displays above the forest canopy, and a rapid, direct, noisy approach to the log in which a triple sound "*Flap-chee-wah*" (*sensu* Skutch 1967), partly mechanical and partly vocal, is emitted. Aldrich and Bole (1937) described the displays as solitary, while Skutch (1967) noted that several males could be present, but that each displayed independently. Rowlett (in Davis 1982) described several males displaying simultaneously, and Slud (1964) ascribed a high degree of coordination among the males. None of the authors saw a copulation or discussed the spatial arrangements of display logs, although Prum (1994) considered the display system of *C. leucorrhoa* to be a dispersed lek.

The other species in the genus, *C. gutturalis*, from northeastern South America, has been studied more extensively by Prum (1986) and Théry (1990, 1992, 1997; Théry and Vehrencamp 1995). This species is very similar to *C. leucorrhoa*, except for the presence of a large concealed white patch on the wing visible when the wing is extended (Prum 1986), the lack of shortened or emarginate outer primaries, and the inability to erect its throat patch into a ruff. *C. gutturalis* males display on mossy logs on the forest floor, arranged in exploded leks 120–250 m in diameter and 230–350 m apart, with a mean distance 38 m between logs of each arena (Prum 1986, Théry 1990). Males apparently hold individual territories more widely separated than in classical concentrated leks and perform competitive displays. In this species, groups of males were observed displaying together, with some of the individuals that displayed habitually in a territorial manner joining group display at other sites as well (Davis 1949, Prum 1986, Théry 1990). Prum (1986) interpreted this behavior as detached or mobile leks, in which "males abandon exclusive display territories for the competitive group display at a series of sites." More extensive observations by Théry (1990) led him to conclude that exclusive territorial behavior is more important than mobile group display, which he attributed more to a period of establishment of individual territories before the breeding period.

The objective of the present study was to examine the relationship between group and individual display in *C. leucorrhoa*. Specifically, we wished to determine whether *C. leucorrhoa* displays in mobile leks, as suggested by Prum (1986), or whether display logs have exclusive owners, as suggested by Théry (1990). For this study, we took advantage of a large banded population and a grid of study area trails from an earlier study on the annual cycle and fruit diet of this species (Rosselli 1994).

METHODS

We conducted the study at Finca el Plástico (10° 18′ N, 84° 01′ W), a private reserve covered mostly by mature forest (premontane wet forest *sensu* Holdridge; Tosi 1969) 6 km south of Las Horquetas de Sarapiquí, Provincia de Heredia, on the Atlantic slope of Costa Rica. The reserve, along with its neighboring parks and protected areas, is part of a continuous forest area of nearly 44,000 ha that extends between elevations of 50 and 2,900 m. Annual rainfall is about 500 cm with a dry season between January and April or May, followed by rains during the rest of the year, peaking in July (for a more detailed description of the study site and bird community, see Rosselli 1989, 1994). We worked mostly in a 12-ha study area crisscrossed with a grid of trails 50 m apart, located in mature forest between 500 and 600 m in steep and varied terrain (Fig. 1). In a previous study (reported in Rosselli 1994), *C. leucorrhoa* had been one of the most abundant understory birds, and 179 individuals had been individually color banded at the site. We therefore did not use mist nets in the present study, hoping to disturb the birds as little as possible.

We spent 34 days in the field between 20 April and 28 May 1989, during which our main activities were censuses in search of display logs and detailed observations from blinds at active display logs. Censuses were conducted by three observers walking slowly along the trails in the study plot and stopping every 100 m for 30–60 min, listening for any call or sound produced by White-ruffed Manakins. Because of the intermittent nature of log activity, only by waiting ≥30 min at a site could we be certain not to miss finding any nearby display logs. Censusing was conducted intensively during the first week and periodically thereafter (9 days in all) to detect any new logs not found previously. We conducted censuses between 07:00 and

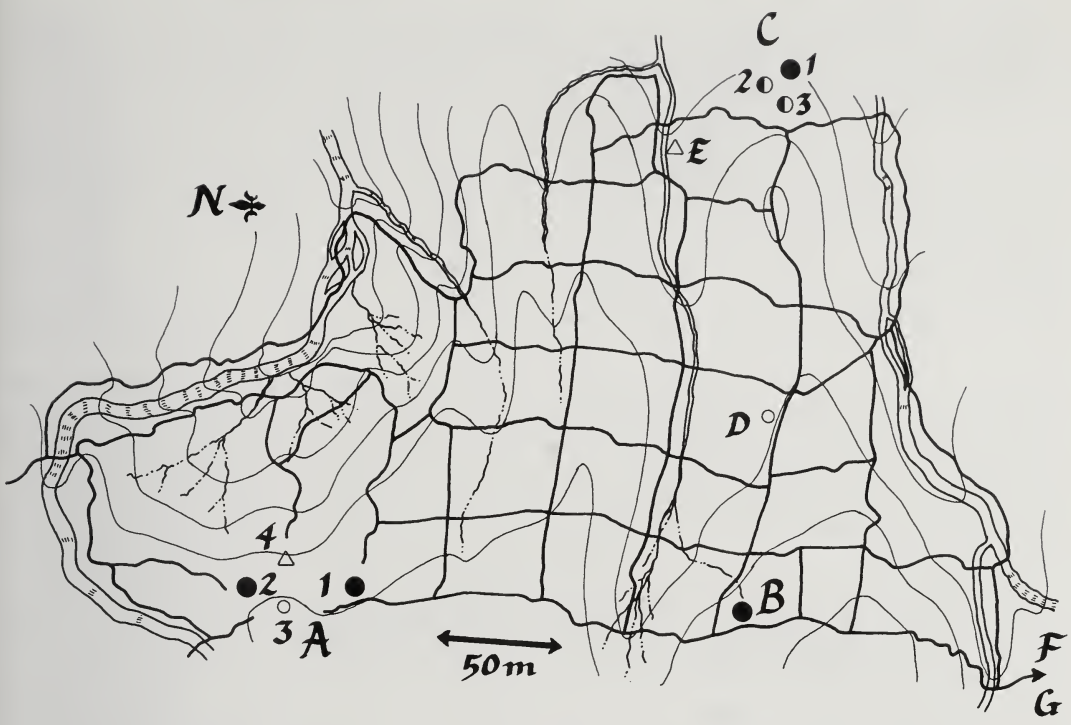

FIG. 1. Topographic map of 12-ha study area in Finca El Plástico (Heredia, Costa Rica) showing trail grid, and permanent and occasional display logs of White-ruffed Manakins (*Corapipo leucorrhoa*) and areas (contour lines denote 10-m intervals of elevation, between 520 and 590 m). Solid circles are logs with banded resident males, half-filled circles are logs with continuous activity but no banded male, open circles are logs without permanent activity, and open triangles are areas with occasional displays but no log. Note that most logs were found in two main clusters (A and C). Data are from 1989.

13:00 along 3 km of trails; each segment was censused 5–6 times. We made observations from dawn to dusk (05:00–17:30, though mostly between 07:00 and 15:30), from blinds constructed with PVC pipe, sheet plastic, nylon screening walls, and fiberglass roofing sheets, set up 4–8 m from the logs. We accumulated 78 h of censuses and 358 h of observations at the logs.

Similarity in appearance made it difficult to distinguish females and first-year males, therefore some green unbanded individuals were considered first-year males according to their courtship behavior and reaction of resident males to them. Only in a small proportion of the visits were we completely sure these green individuals were females, either because they had been color banded previously or because they copulated with a male. We considered as females the other green individuals that behaved in the "secretive" way typical of the banded ones and elicited a courtship response in the male or males present.

Although censuses and observations were conducted mainly in the study area, we also spent nearly 40 h exploring and observing outside the plot. Our observations were focused on four of the active logs (A1, 65.5 h; A2, 82.5 h; B, 78 h; C1, 31 h); each of the other logs was observed for 5.5–20.9 h. At the four main display logs, we made video recordings with a Canon 8-mm XM-E708 camera. We completed about 4 h of recordings that contain most of the elements of the display behavior of *C. leucorrhoa*. With the help of F. G. Stiles we also obtained sound recordings of the more common vocal and mechanical sounds emitted by the manakins with a Uher 4000 Report-L tape recorder. Subsequently, sonograms were made from the recordings by J. W. Hardy at the sound laboratory of the Florida Museum of Natural History.

RESULTS

Description, density and location of display logs.—We found eight logs on the study area at which male *C. leucorrhoa* displayed (Fig. 1). Four of these logs (A1, A2, B, and C1) each had a resident banded male that remained in the vicinity from 41–94% of the time, mainly alone (Table 1). At two (C2, C3), there was continuous activity, but the possibly resident males were not banded so we could not confirm their presence, and at two more (A3, D), we occasionally observed *C. leucorrhoa*

TABLE 1. Behavior of White-ruffed Manakins (*Corapipo leucorrhoa*) at display logs during 5-min observation periods, El Plástico, Costa Rica, April–May, 1989. Female visits were directly related to the resident's time alone at a log, and inversely related to the rates of visits by other males and advertisement calls.

	Display log			
	A1	A2	B	C1
Time resident at log (%)	67.8	40.7	79.4	93.7
Time resident alone at log (%)	61.4	39.1	73.4	46.6
Female visits/h	0.2	0.1	0.2	0.1
Other male visits/h	0.3	0.8	0.5	2.5
Advertisement calls/h	25.0	27.7	34.0	109.7

displays, but no individual was seen regularly at the site. We also detected sporadic displays and/or display calls in two areas where no log was found (A4, E). In addition, we found two more logs (F, G) about 1 km south of the study area. These two "foreign" logs were separated by nearly 80 m.

Considering only the continuously active (permanent) logs, the log density in the study plot was 0.5 logs/ha and the mean distance between logs (all pairwise distances) was 182.8 m ± 110.6 SD. Most of the logs and display sites in the plot were arranged in two main clusters (Fig. 1). The mean distance between logs within clusters was approximately 27 m. According to observations by LR and F. G. Stiles (pers. comm.), some of these logs (A2, B) had been used during previous years, and some others that had been active during the 1988 breeding season were not active in 1989.

The White-ruffed Manakins displayed over horizontal portions of fallen trees or live lianas lying on the ground or ≤40 cm above it. The total length of these logs and lianas (hereafter we refer to all simply as logs) ranged from 3.8 to >50 m (in some lianas that came down from the canopy). The manakins used specific, moss-covered portions of these logs, varying between 0.5 and 1.3 m in length. The diameter of the logs varied between 10 and 44 cm, and compass orientation was different for all of them. The part of the log on which the manakins displayed generally was clean and free of obstacles, except on one trunk, where a slender (0.5-cm diameter) vine that the resident male frequently tried to remove crossed the display area perpendicular to the trunk. The manakins actively cleaned the logs by removing fallen leaves and debris, a behavior called "gardening" in other species (Snow and Snow 1985, Prum and Johnson 1987). The area immediately surrounding the logs was free of obstructions, but the configuration of the vegetation surrounding this display area was variable between logs. We found no visually consistent pattern of canopy foliage around the display logs, and no consistent pattern of fruit availability in the immediate vicinity.

Activity at the logs.—The activity pattern at the active logs was similar for the four logs observed at length. Each log was owned by a single adult male (the resident) that remained close to it most of the day from dawn to sunset. Although most residents remained by themselves most of the time, they all had almost daily visits from other males and, less frequently, from females (Table 1). When the resident males were alone at the log areas, they spent their time on 4–6 perches a few meters from the display area, regularly giving a high (3.7–6.2 kHz) short (0.28 s) trill "tree" note or advertisement call (Fig. 2a). This note also was given away from the display logs during feeding and by females. The rate of advertisement calls was 25–34/h, except for log C1 where calls were more frequent. Log C1 also was atypical in having a very high rate of visitation

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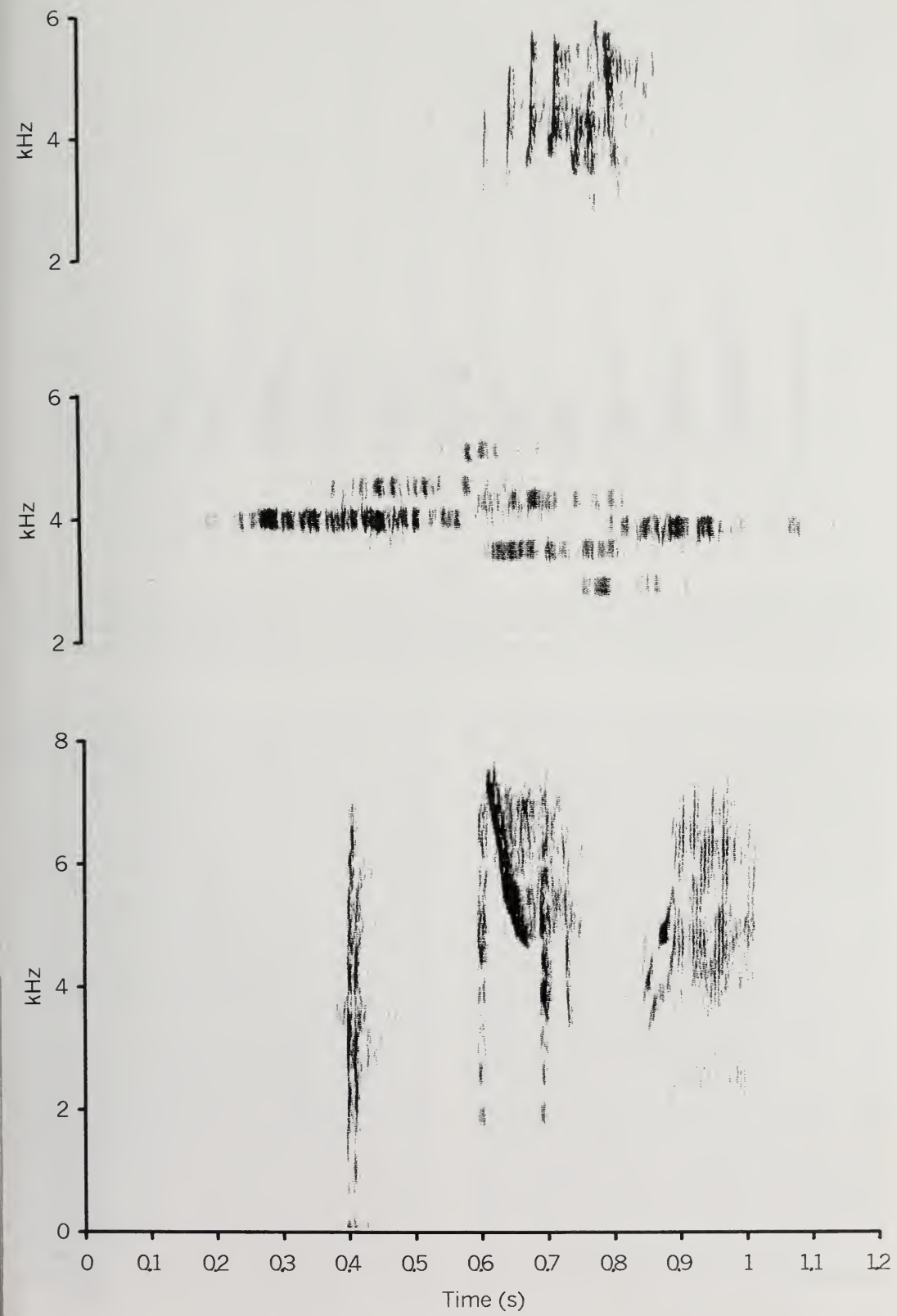
FIG. 2. Sonograms of White-ruffed Manakin (*Corapipo leucorrhoa*) vocalizations. (Top) Advertisement call or trill; (middle) warble or "nurrt," possibly given by more than one male; (bottom) *Flap-chee-wah*. Recordings were made by F. G. Stiles, El Plástico, Costa Rica, May 1989. Sonograms were made on a Kay Elemetrics Model 7029A Sona-Graph, with bandwidth set at 300 Hz.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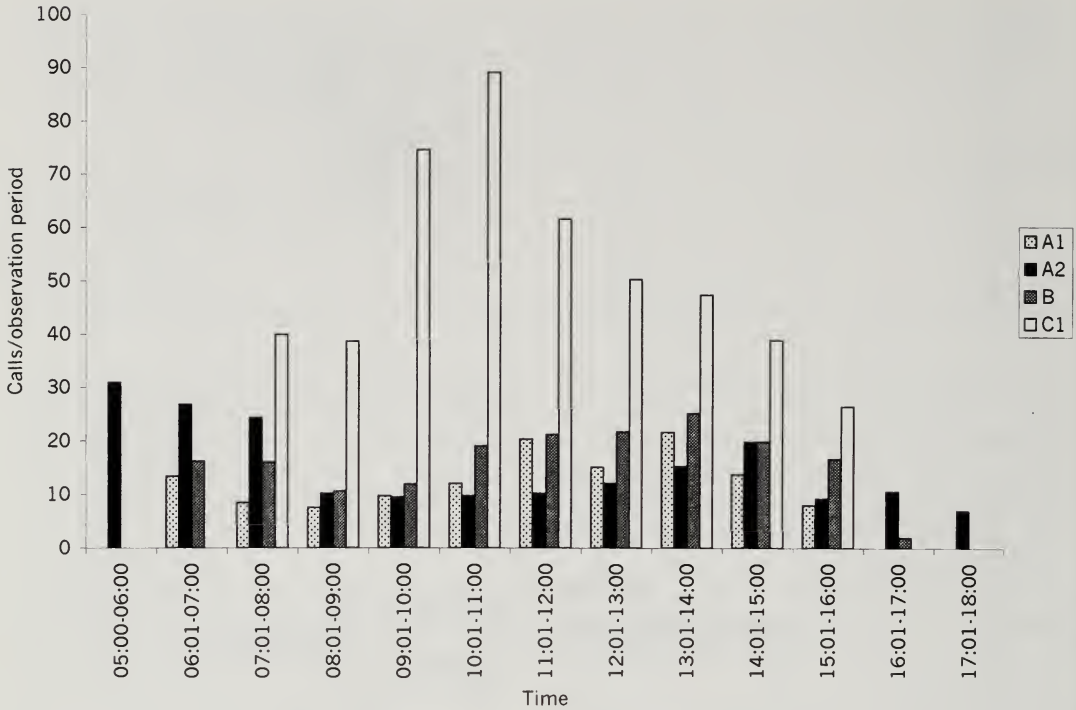

FIG. 3. Daily rhythms of calling intensity at display logs of White-ruffed Manakins (*Corapipo leucorrhoa*) on the study area, El Plástico, Costa Rica, April–May 1989. In three (A1, A2, and B) of the logs the numbers of advertisement calls per observation period was highest early in the morning and early in the afternoon. Log C1 was atypical in several respects, including the highest calling activity late in the morning.

by other males and, along with A2, the lowest rate of female visits (Table 1).

Resident males constantly moved between perches and frequently preened. They commonly left the area for short periods (generally <10 min), apparently to feed or bathe since they often returned with fruit in their bills or with wet plumage. The rate of advertisement calls through the day was similar for logs A1, A2, and B, with a peak early in the morning (06:00–08:00), a period of relative low activity between 08:00 and 10:00, and a steady increase thereafter until 14:00. At log C1 there was a pronounced peak between 10:00 and 11:00; we have no observations before 07:00 or after 16:00 (Fig. 3). The total number of calls on a single day ranged from 215 during 9 h of observation at log A1 to 1,377 during 8 h of observation at log C1. The rate of calls per observation period was <40 calls/h at logs A1, A2 and B, and 109.7/h at log C1 (Table 1).

Visits from other males, movements and associations.—The 200 observed visits from males (other than the resident) at the display logs took place mostly in the mornings and mainly before 08:00 at logs A1, A2 and B. At C1, the number and rate of visits was much higher and peaked between 09:00 and 10:00 (Fig. 4, Table 1). The visits included males of different ages (first and second year, and adults) that usually came in groups of ≤6 individuals. Visiting males seemed excited and nervous, and displayed actively. The resident males sometimes took part in the displays. We also observed aggressive behavior between males (see below).

We heard one type of vocalization exclusively during these visits, when there was >1 male at the display log area. This was a longer trill similar to a warbling note "currrrtrrr," between 2.5 and 5 kHz and up to several seconds in duration (Fig. 2b). When a group of males emitted this "warble" they stood very close to each other, sometimes only a few centimeters away on the same branch. We had the impression they were attracted to each other

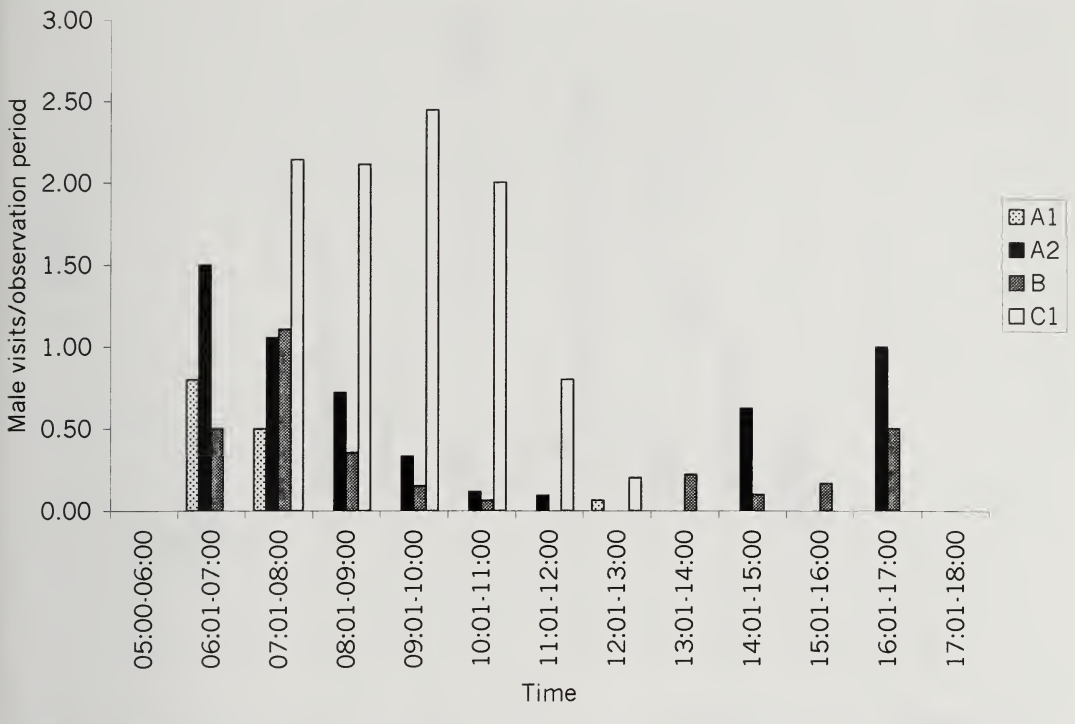

FIG. 4. Visits by nonresident males per 30-min observation period through the day at display logs of White-ruffed Manakins (*Corapipo leucorrhoa*), El Plástico, Costa Rica, April–May, 1989. Most visits occurred during early morning at logs A1, A2, and B, but at log C1 a very high visitation rate occurred during late morning.

while warbling. The resident male warbled with visitor males.

Besides numerous observations of unbanded females, young, and adult males, we detected 32 individually banded males (44% adults, 56% immatures) and 4 females during our observations. Twenty of these individuals (including the resident males of logs B and C1) were seen at only one of the display sites, seven at two sites, and five at three sites. Most of the movements between different display sites were made among adjacent sites; nine of the individuals seen on 2–3 different logs were concentrated in either the A or the C clusters, with maximum distances of 41 m and 11 m between logs, respectively. Three nonresident males made the longest recorded movements (300 m between B-0 and C1, 200 m between A2 and B, and 51 m between the E area and logs C3 and C2). Also, the resident male of log A1 occasionally visited logs A2 and A4 and displayed (see Fig. 1).

On 16 occasions we saw groups of males, including ≥2 banded individuals, visiting the display logs; only three combinations of two banded males were seen together twice, the rest were different combinations of males in each cluster. Therefore, we found no indication that these were coherent groups. The visits to the logs lasted from <5 min to >5 h. We do not know where these visitors went later in the day.

At log A2, there were more visits at the beginning than at the end of the study. The resident started to spend much of his time at a new log (A3) 10 m away from the original one on the last days of our observations. The male displayed and was visited by a female at the new log.

Female visits.—"Females" visited all the active logs. We recorded 34 such visits to the four logs studied most intensively. Log A1 had the highest rate of female visits and logs A2 and C1 had the lowest (Table 1). Females visited the logs mainly between 09:00 and 15:00 when resident males were alone, except for log C1 where the few visits observed came

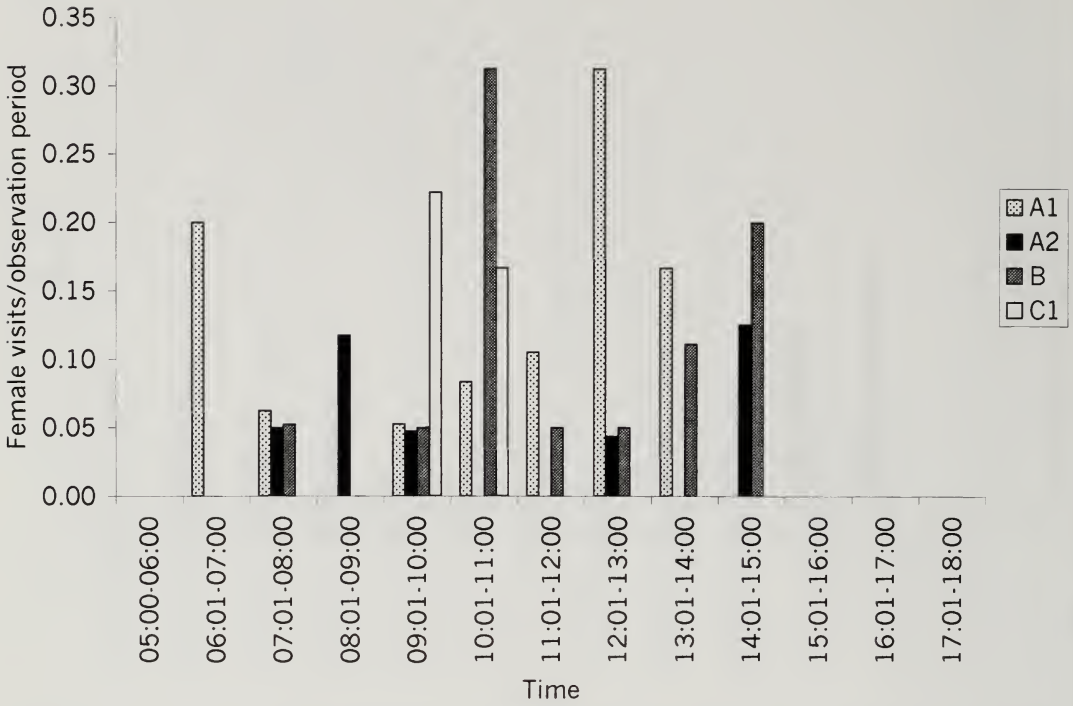

FIG. 5. Visits by females per 30-min observation period at display logs of White-ruffed Manakins (*Corapipo leucorrhoa*), El Plástico, Costa Rica, April–May, 1989. Most visits occurred 09:00–15:00 when there were few visits by nonresident males.

during a period of higher visitation by other males (09:00–10:00; Fig. 5).

Behavior at the display sites.—Besides perching around the log during most of the day and giving advertisement calls, resident *C. leucorrhoa* males performed several visual displays, some with associated sound:

Flap-chee-wah.—This was the most elaborate and spectacular display we observed. It was performed by resident males either alone or in the presence of females or other males. It also was performed by visiting males and, on several occasions, two or more males (including the resident) appeared to perform the *Flap-chee-wahs* in a coordinated manner.

In this display, the performing bird flew to the display log, then flew steeply upward, often in a spiral. At approximately the high point of the flight, 1–3 extremely high, thin notes (Canopy calls) were heard in about 34% of the times. We strongly suspect, judging from the far away quality of the notes and the fact that we invariably lost sight of the birds as they entered the canopy, that the birds flew straight up to above the canopy to give these notes. About 2–3 s after giving these notes, the displayer plummeted diagonally down to the display log at very high speed and landed, facing the opposite direction from the ascent; instantly the bird jumped about 10–90 cm, turning in the air to land facing the original landing point (Fig. 6). After this second landing he sometimes remained crouched flicking his wings, or he sometimes immediately flew from the log. When another bird was perched on the log, the displaying male landed facing it in each case. At about the moment the bird first landed on the log a loud, explosive snap or "flap" noise was produced, followed immediately by one or two high notes ("chee" or "chi-chi") and a sharp buzzing note ("waa" or "wheew"; Fig. 2c).

These notes were produced so rapidly, and the landing and jump were so nearly instantaneous, that it was impossible to determine exactly the relationship between the sounds and the jump. The "flap" apparently is a nonvocal sound, possibly produced by the modified primaries (Prum 1998); the "chee-waa" may be vocal. When a displaying bird landed on the

FIG. 6. Complete *Flap-chee-wah* display sequence of White-ruffed Manakins (*Corapipo leucorrhoa*), El Plástico, Costa Rica, April–May, 1989. Ascending flight, flight over the canopy with Canopy calls, and explosive landing on the display log and rebound (accompanied by "Flap-chee-waah" sound).

log following the jump, his throat feathers were strongly fluffed, but it was not possible to determine whether the throat was puffed out during the entire display. The directions of departure on the upward spiral, and arrival at the log, were constant on all *Flap-chee-wahs* performed at a given log. Generally a *Flap-chee-wah* was preceded by apparent nervousness, rapid flights between nearby perches, and landings on the display area of the log by regular flight or any of the special flights (Butterfly, Undulating) described below.

When several males performed simultaneous displays, the male that had landed in a *Flap-chee-wah* remained in a crouched position on the log, flicking his wings and looking up, as if waiting for the next male to land; when a second male landed, the original male usually flew away from the log and this second individual would remain on the log similarly "waiting" for a third *Flap-chee-wah*. Sometimes the displaying males remained on the log and up to three males would be perched on the log at the same time. Rapid sequences of several *Flap-chee-wahs* were observed on several occasions with birds almost landing on top of each other.

Each element in the display (nonvocal sounds, vocal sounds, spiral ascending flight, rebound, Canopy calls) could be present or absent on a given occasion. The elements more commonly present were a landing at the log, followed by an upward flight, and the explosive landing with the *Flap-chee-wah* sound.

We detected no differences in the performance of displays between adult resident males and young visiting males; both performed complete display sequences and incomplete "practice" displays in which the calls or nonvocal sounds were different or the

FIG. 7. Butterfly flight based on video images of White-ruffed Manakins (*Corapipo leucorrhoa*), El Plástico, Costa Rica, April–May, 1989.

jump was slow. Once we saw an immature individual crashing against some leaves in a display attempt at log G. We observed a total of 252 *Flap-chee-wahs*. Most (66.3%) of these displays were performed by 12 banded males, including the banded residents (56.7%). On 77 occasions the display was performed by unbanded adult males and 8 times by unbanded green individuals.

Butterfly flight.—This is a very stereotyped flight performed by males flying to or from the display log, or between low perches nearby. The flight is slow and undulating, the body held in vertical position with the plumage fluffed; in particular the throat is fully puffed out (Fig. 7). The Butterfly flight was almost always associated with the presence of a female or other males in the display area. No sound was emitted during this display; in fact, the flight was notably silent, the birds seeming to float like little black and white pompons.

Undulating and Rapid flights.—Another flight that probably was a variant of the Butterfly flight was the Undulating flight in which males would oscillate up and down, although with less pronounced waves and their body and plumage in normal position. Sometimes the birds also performed straight Rapid flights nervously between the display log and nearby perches. Frequently before or after these Rapid flights males emitted a loud or subdued snapping sound "plop" or "flap" either in flight or on a perch. This sound was nonvocal, and probably produced with the wings, and also could occur as a single event or in association with other displays.

Throat-flagging.—This display consisted of a slow, stereotyped head movement performed by males perched on the display log, evidently to show off the throat feathers, which were fully erected to form a dense beard (Fig. 8). Facing diagonally toward the center of the log, with his head held low and horizontally, the male slowly rotated his head sideways through an angle of about 30–45°, so that one eye faced diagonally downward toward the log, the other diagonally upward; this head movement was accompanied by a single rapid flicking open-and-closed of both wings. The male then would repeat the head movement in the opposite direction. This display usually was performed following a But-

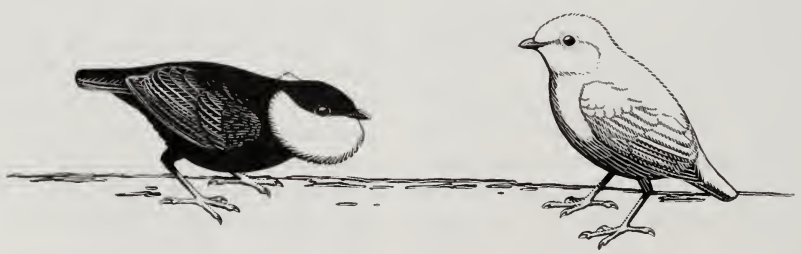

FIG. 8. Throat-flagging display performed on display logs by male White-ruffed Manakins (*Corapipo leucorrhoa*), El Plástico, Costa Rica, April–May, 1989.

terfly flight, but also sometimes following *Flap-chee-wahs* or Rapid flights; it usually was directed at other birds (males or females) but occasionally was performed in the absence of other birds as well.

On many occasions a male, usually alone, was seen to move his head as if looking at the log with one eye and then the other, or look down as if looking at his feet, but not in the slow, stereotyped way described above and without the erected ruff. We believe this might be a variant of the Throat-flagging. Occasionally the residents displayed without any obvious reason.

Courtship of females and copulation.—The female visits to the logs lasted from a few seconds (in which cases the females probably were merely passing through the area) to >10 min, when they were visibly interested in courtship. The females typically arrived quietly, perching at heights ≤1.5 m on vertical stems of shrubs or saplings in the understory. Males reacted to their presence with fast movements and numerous Rapid and Butterfly flights to the display log or between perches. After each landing the males performed the Throat-flagging display. The female then began to follow the male on some of these flights, sometimes appearing to chase him. If the female landed on the log, the male continued with Rapid flights and Butterfly flights to and from the log for ≤12 min, each time landing 10–20 cm in front of her and Throat-flagging. During these periods we recorded 16–46 Rapid flights and 6–70 Butterfly flights. Finally, with the female perched on the central part of the display area on the log, the male would depart in the upward Spiral flight; the high thin *tsee* notes or Canopy calls were heard from above 75% of the times (compared to 34% when there was no female present), and the male would land with a *Flap-chee-wah*. If the female still remained on the log, he would land on one side of her, jump over her and land on the opposite side, then immediately hop toward her and mount; copulation lasted only about 2–3 s, then the female flew away.

We observed two sequences that terminated in copulations: one by the resident male at the C-0 log on 1 May the other by an unmarked adult male, presumably the resident, at the F log on 23 May. In both cases no other males were present and the sequence of displays was as reported above. Many other sequences we observed did not end in copulation because the female departed. The female would abandon the area at any point of the described sequence; in several cases, she departed after the male had flown up toward the canopy during the final *Flap-chee-wah*.

Both copulations occurred relatively late in the day (12:45 and 14:47, respectively); indeed, most female visits occurred after 09:30 when the resident males were alone. The presence of other males, as often occurred early in the morning, might have disrupted courtship activities. We noted an apparent example of this several minutes after the copulation at log F. About 5 min after the copulation, a presumed second female arrived. The male performed several Butterfly flights, and the female landed on the log. When the male flew up to perform a *Flap-chee-wah*, a second-year male landed on the log in front of the female and performed the Throat-flagging display to her. At that moment the first male landed and the three individuals flew away; a similar situation was described by Davis (1949) for *C. gutturalis*.

If a female visited a log when more than one male was present, all the males performed courtship displays, including Butterfly flights and Throat-flaggings, and they also moved nervously and rapidly between perches. In most cases males chased each other and we saw no copulations on these occasions.

Aggression.—We saw three types of aggressive behavior. Chases occurred mainly between males of all ages when they were together at a log. They could be very long (>1 min) in the vicinity of the log. These chases and displacements were very fast and most of the time we could not see if the individuals were banded, but on one occasion at log C1 we saw that the resident male was the individual who was chasing an intruder, and in two other occasions we saw adult males chasing immatures. We also saw groups of immature males present at the log and chasing each other in the absence of the resident.

Attack behavior was typical of the resident male at log B, although occasionally seen in others. This individual was very aggressive toward other birds (including hummingbirds and thrushes) that approached his territory around the log when he was alone. He would

rush suddenly toward them producing a low "grraaahh" or "cuaak" sound. However, he never attacked the other *C. leucorrhoa* males that visited him early in the morning.

Displacements frequently occurred in the series of displays when there were several males present. A male could land and displace another on the log or on a nearby perch.

DISCUSSION

This study provides both new observations and confirmation of some previous ones on this species. Previous studies did not have the advantage of having such a large number of banded individuals; thus we were able to clarify several incongruencies, such as the ownership of logs, the identities and movements, and relations between nonresident or subordinate individuals, and the nature and possible role of groups of males at the display sites. We found that *C. leucorrhoa* displays in loosely aggregated display territories or dispersed or exploded leks (Foster 1983, Prum 1994), although this is quite variable among individuals. Nevertheless, some of the display logs observed seemed to be visually or auditorily isolated from those of other males, as stated by Aldrich and Bole (1937). The mean distance between logs in a group and between groups of logs or leks was similar to what Théry (1992) found for *C. gutturalis* and Snow and Snow (1985) found for *Ilicura militaris*.

As Slud (1964) and Skutch (1967) observed, several juvenile and adult males may visit and display at the same log although according to our observations, they do not own or share the log permanently as stated by these authors. Rather, they are permitted to visit, especially at some times of the day, apparently as a social function related to establishment of a hierarchy as proposed by Foster (1983). Théry (1990) also found this to be the case in *C. gutturalis* in French Guiana. These visits also occur in *Ilicura militaris*, a group closely related to *Corapipo* according to Prum (1990, 1992) with which it shares several other display elements including the nonvocal "single snap or flop" in flight found during this study.

We found that each log belonged to a single resident male who spent most of his time in its vicinity and had priority for copulation with females. The most successful log (with most female visits and one of the two copulations observed) also was the one with fewer male visits. This suggests that the establishment of a hierarchy, both by ritualized displays such as the warbling calls and the consecutive *Flap-chee-wahs*, and with more obvious aggressions such as chases, attacks and displacements, probably is the most important role of the multimale activity at the logs during the morning. The enhanced activity and sound also could make the logs more attractive to females. However, most female visits, including some that resulted in copulations, occurred when residents were alone, and our observation of a disruption could indicate that females avoided times when more than one male was present at the display site.

The early morning visits of numerous males could be a daily re-establishment of the hierarchy. This could reinforce the dominance of the resident males and assign a rank order to the visitors and put them in a "waiting list" to take over the log or logs that a group visits in case the resident disappears. The fact that some observers saw only single males (Aldrich and Bole 1937) or only groups (Slud 1964, Skutch 1967) displaying might be due to the times of day in which the observations were made. A similar peak of aggressive activity in early morning, with female visits and copulations later in the day, was found in Long-tailed Hermits (*Phaethornis superciliosus*; Stiles and Wolf 1979).

Prum (1986) found a similar situation of dominance by an individual and "moving" groups of male visitors in the White-throated Manakins in Suriname. Based on our banding data we demonstrated that these flocks were not permanent social assemblages, but of changing composition day to day. These data also permitted us to conclude that most individuals moved little between logs and then usually only for short distances.

The great variation found in spatial aggregation and activity schedules among the logs studied probably reflected different stages in the establishment of a hierarchy. Cluster C probably was in an early stage since it was not detected during previous years and there were high rates of male visitation and male-male interactions together with a low rate of female visits. Cluster A differed in that one of its logs (A1) had a well-established and suc-

cessful resident while its neighbor (A2) was in an unstable situation in which the resident divided his time between two logs (A2 and A3). These tangential logs near A1 and C1 might be similar to the peripheral courts in which an intruder male *C. gutturalis* that often visited residents displayed erratically (Théry 1992). Log B, isolated during the mating season, might have had a highly aggressive male who had been effective in maintaining his dominance or the momentary situation in a system that changes considerably over time. Prum (1986) found in Suriname a similar localization of the logs in "loose groups" and "solitary situations" in *C. gutturalis*.

We do not know if the rapid sequences of *Flap-chee-wahs* performed by several males when present at the same log was the result of a coordinated display or if the "turns" they took displaying were simply to avoid crashing into each other; as Skutch (1967) observed, there otherwise was no coordination or synchronization present and males displayed simultaneously and independently at a log. The situation found in *C. leucorrhoa* in which several males engaged in possibly coordinated ritualized displays denotes similarity between *Corapipo* and *Chiroxiphia*, although in *Corapipo* there is no true cooperation in which the subordinate males contribute to the attraction of females to the group and more than one male is required in the display (Foster 1977). A close relationship between *Chiroxiphia* and *Corapipo* has been proposed by Brumfield and Braun (2001) based on electrophoretic methods. In *C. leucorrhoa*, visitors neither travel together nor visit the same log regularly, although they apparently do not move extensively in the area and remain in the vicinity of one established display site. Prum (1986) saw the same unsynchronized displays in *C. gutturalis*, although the groups of males moved together to nearby logs to continue with the displays. Brumfield and Braun (2001) also proposed *Antilophia galeata* to be closely related to *Corapipo*. Poorly known, *Antilophia* is the only manakin in which the lek or arena display behavior has been lost and males establish an extended pair bond with females, although they are highly aggregated and territorial (Marini and Cavalcanti 1993, Prum 1994), so far the only behavioral similarity found with *Corapipo*.

Various elements of the displays of *C. leucorrhoa* appear to be shared with *C. gutturalis* (Davis 1982; Prum 1986; Théry 1990, 1992), including the high trill or Advertising call, the *Flap-chee-wah* display, and the Canopy calls or Flight Song display. *C. gutturalis* possesses two displays not found in *C. leucorrhoa*: a posture in which they "raise their bill vertically and erect a small puff of white feathers at the base of the throat patch" (Prum 1986) and the displays in which they show the white wing patch (absent in *C. leucorrhoa*). Copulations in *C. leucorrhoa* seem to be very rare events, as also was observed by Théry (1990) in *C. gutturalis*. In both species copulation occurred when only one male was present (but see Davis 1949), and happened after a series of flights between perches in which the female could participate followed by a full sequence of a flight display and explosive landing on the log, the male jumping over the female before mounting her. However, in *C. gutturalis* the male landed facing away from the female, and in *C. leucorrhoa* the male landed facing her. In *C. leucorrhoa* the female did not touch the tips of the male's primaries with her bill as was seen in *C. gutturalis* before the three copulations observed by Théry (1990); we did not notice any possible signal of acceptance of copulation from the female. The low number of copulations in El Plástico also could be related to the low female:male ratio found in the area all year long, including the mating season (Rosselli 1994).

We found striking similarities between *C. leucorrhoa* and *Masius chrysopterus* (Prum and Johnson 1987), such as the countersinging or "nurrts" between the resident male and visitors. The Throat-flagging display, previously unknown in *Corapipo* (Prum 1994, Prum and Johnson 1987), seems very similar to the side-to-side bowing display of *Masius*. This, added to the similarity in the structure of the display calls and the fact that in *C. leucorrhoa* as well as in *Masius* some males display "faithfully" at a site in a territorial manner, while others are quite transient in their patterns, support Prum's (1990) phylogenetic analysis that places these genera close together.

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NESTING SUCCESS OF THE GREAT CRESTED FLYCATCHER IN NEST BOXES AND IN TREE CAVITIES: ARE NEST BOXES SAFER FROM NEST PREDATION?

KARL E. MILLER[1,2]

ABSTRACT.—Although it is commonly believed that nest boxes yield artificially high estimates of nest success, few investigators have compared nesting success in nest boxes to tree cavities in the same locality during the same time period. I studied nesting success of Great Crested Flycatchers (*Myiarchus crinitus*) breeding in nest boxes and natural sites (i.e., old woodpecker cavities and natural tree hollows) on the same pine plantations in northern Florida. Mayfield estimates of nesting success were nearly identical between nest boxes (0.37 ± 0.05 SE, n = 32 nests) and tree cavities (0.38 ± 0.06 SE, n = 27 nests) during a 2-year period. However, nesting success was greater in nest boxes (0.53 ± 0.06 SE) than in cavities (0.33 ± 0.10 SE) during 1997 and lower in nest boxes (0.26 ± 0.07 SE) than in cavities (0.42 ± 0.09 SE) during 1998. Lower nest success in nest boxes during 1998 was due to increased predation during the incubation period. Nest predation accounted for ≥83% of all nest failures. Documented nest predators included the southern flying squirrel (*Glaucomys volans*) and corn snake (*Elaphe guttata*). Nest boxes and cavity nests did not differ significantly in any habitat variable that would influence nest concealment, nor did these variables differ significantly between years. Evidence suggests that nest predators may learn to exploit nest boxes as a prey resource, either through the development of search images or through long term spatial memory. This study demonstrates that nest boxes are not always safer sites than tree cavities and that static comparisons may give misleading results. *Received 30 July 2001, accepted 25 March 2002.*

Ornithologists have used nest boxes to study avian life histories and population dynamics for more than half a century. However, the use of nest boxes as research tools has been criticized (Møller 1989). Some have argued that nest boxes are safer from predators than natural nest sites and that patterns of reproductive success observed in nest box studies may be an artifact of nesting in boxes (Nilsson 1984, 1986; Møller 1989; Purcell et al. 1997). However, there have been few rigorous field tests of these assumptions. Many studies that purport to show differences between nest boxes and tree cavities have compared separate populations in different locations (e.g., Lundberg and Alatalo 1992, Kuitunen and Aleknonis 1992), while ignoring spatial and temporal differences in habitat quality and predator density. Within a given species, reproductive success can vary considerably over space and time among nest sites (e.g., Nilsson 1975, 1984, 1986; Korpimäki 1984; Alatalo et al. 1988; East and Perrins 1988), prohibiting generalizations about differences between nest boxes and tree cavities.

Few studies have compared the nesting success of birds in nest boxes and tree cavities in the same locality during the same time period, and the results from these have been inconclusive. Although some studies reported higher nesting success in nest boxes (Nilsson 1975, 1986; East and Perrins 1988), others indicated no differences (Robertson and Rendell 1990, Gehlbach 1994) or higher nesting success in cavities (Ritter et al. 1978). Moreover, when differences were found between nest boxes and natural sites, there was no consistent pattern for all cavity-nesting species in a particular study area (Nilsson 1984, Purcell et al. 1997). Furthermore, nest boxes and tree cavities can differ in other respects that often are not measured. Because nesting success of cavity-nesting birds can be correlated with nest height (Nilsson 1984, Li and Martin 1991) and microhabitat structure (Belles-Isles and Picman 1986, Finch 1989), these factors also need to be measured when comparing nest boxes and tree cavities.

My objective in this study was to compare nesting success of Great Crested Flycatchers (*Myiarchus crinitus*) using nest boxes and tree cavities in the same habitats during the same years.

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METHODS

Study site and study species.—I conducted my study in 35- to 40-year-old slash pine (*Pinus elliottii*) plantations at Camp Blanding Training Site, a Florida Army National Guard facility in northern Florida (30° 00′ N, 82° 00′ W). My field assistants and I monitored nests in tree cavities on twelve 10-ha pine plantation study plots, one 8-ha pine plantation study plot, and one 15-ha pine plantation plot that included patches of turkey oaks (*Quercus laevis*). All study plots were even-aged pine stands lacking a well-developed understory (see Miller 2000 for further description of plant communities). Density of standing dead trees (snags) in these stands ranged from 13–19 per ha. Most snags were <26 cm diameter dbh, decayed rapidly, and persisted for only a few years.

The Great Crested Flycatcher was the most common secondary cavity-nester (i.e., nonexcavator) species on the study area. It is migratory, returning to the study area each year during the last week of March. The Great Crested Flycatcher is single brooded but will renest if its first nesting attempt of the season fails (Lanyon 1997; KEM pers. obs.). Potential nest predators in the study area included the southern flying squirrel (*Glaucomys volans*), cotton mouse (*Peromyscus gossypinus*), corn snake (*Elaphe guttata*), yellow rat snake (*Elaphe obsoleta*), and Blue Jay (*Cyanocitta cristata*).

Nest boxes.—I placed 160 nest boxes on eight of the study plots (20 nest boxes per plot) during late February and early March, 1997. Nest boxes were constructed of rough-cut cedar with an entrance hole (5.1 cm diameter) appropriate for Great Crested Flycatchers. Although the entrance hole allowed occasional use by smaller species, such as the Tufted Titmouse (*Baeolophus bicolor*), Carolina Wren (*Thryothorus ludovicianus*), and Eastern Bluebird (*Sialia sialis*), only the Great Crested Flycatcher commonly used nest boxes. I placed nest boxes on live pine trees at 50-m intervals within each plot, alternating the heights between 1.8 m and 4.8 m above ground. All nest boxes were oriented with the entrance hole facing east by southeast, as an easterly or southeasterly orientation often is preferred by many cavity-nesting bird species (e.g., Conner 1975, McEllin 1979, McFarlane 1992, Rendell and Robertson 1994). I placed each nest box so that the entrance hole was not obscured by vegetation for >1.5 m in all directions.

Nest box monitoring.—I inspected each nest box at least once every 10–14 days during April and May and at least once every 14–20 days during June and early July. As soon as I found nesting activity by Great Crested Flycatchers, I monitored the nest box at 3–4 day intervals. I recorded all other species that occupied nest boxes. Southern flying squirrels were not evicted from nest boxes because they routinely used the same size tree cavities as Great Crested Flycatchers (pers. obs.), and I did not want to bias my comparison of nesting activities in nest boxes versus tree cavities. Because flying squirrels also are potential nest predators, I counted all squirrels observed in each nest box during monitoring visits to assess if flying squirrel densities changed over time. I defined primary roost sites as those nest boxes in which flying squirrels were observed on ≥2 occasions within a season.

Cavity nest monitoring.—I used standard methods (Martin and Geupel 1993) to search for Great Crested Flycatcher nests from mid-April through early July of 1997 and 1998. I also searched a buffer strip approximately 75 m wide around each study plot to ensure that birds breeding on the edges of plantation plots were monitored. I rotated nest search visits among plots and diel periods (early morning, late morning) to maintain comparable search effort among sites. As soon as a cavity nest was located, it was monitored at 3–4 day intervals (Martin and Geupel 1993, Ralph et al. 1993). Nests located <4 m above ground were reached with a stepladder and the contents observed with a light and dental mirror. During 1997, most cavities >4 m high were monitored from the ground through observation of adults carrying nest material or food into the cavity, although I investigated a few cavities in larger, more stable snags with Swedish sectional tree-climbing ladders. During 1998, I monitored all cavities >4 m high with a video probe mounted on a telescoping fiberglass pole (TreeTop II, Sandpiper Technologies, Inc., Manteca, California). I considered nestlings to have fledged if they were alive when checked within 1 day of expected fledging and subsequent checks showed no evidence of predation or disturbance to the nest (Martin et al. 1997). I visited most nest territories 1–2 days after the expected date of fledging to confirm that fledglings were present.

Nest-site characteristics.—I measured structural variables within 0.01-ha circular plots (5 m radius) centered on nests, including percentage of bare ground, percentage of ground covered by grass, percentage of ground covered by shrubs, mean shrub height, mean palmetto (*Serenoa repens*) height, and number of stems 2.5–8.0 cm diameter dbh. Within 0.4-ha circular plots (11.3 m radius), I measured the number of small trees (8–15 cm dbh), total basal area (m^2/ha), canopy height, and midstory height. Methods for collecting habitat data follow Martin et al. (1997).

Statistical analyses.—In analyses of nesting success, I used 14 days and 15 days for the length of the incubation and nestling periods, respectively (Taylor and Kershner 1991; KEM unpubl. data). The day the last egg was laid was considered the first day of incubation. For cavities that were too high to be inspected, I estimated the first day of incubation through observation of parental behavior at the nest (Martin and Geupel 1993). I considered a nest to be successful if it produced ≥1 fledgling. I calculated nesting success rates with the Mayfield method (Mayfield 1961, 1975) as modified by Hensler and Nichols (1981) and Hensler (1985), and tested for differences in nesting success between years and between nest types with one-tailed, standard normal Z tests. I used a Wilcoxon signed rank test (SAS Institute, Inc. 2001) to compare flying squirrel numbers in nest boxes between 1997 and 1998; I

TABLE 1. Mayfield nesting success rates for Great Crested Flycatchers (*Myiarchus crinitus*) using nest boxes, Camp Blanding Training Site, northern Florida.

	Incubation period (14 days)		Nestling period (15 days)		Overall (29 days)	
Year	*n*	Success (SE)	*n*	Success (SE)	*n*	Success (SE)
1997	12	0.917 (0.079)	11	0.578 (0.037)	12	0.531 (0.057)
1998	20[a]	0.446 (0.114)	10	0.582 (0.041)	20	0.260 (0.069)
	$Z = 3.40$, $P < 0.001$		$Z = 0.07$, $P = 0.47$		$Z = 3.03$, $P = 0.001$	

[a] Eight (40%) of these nests were preyed upon within the first 6 days of the incubation period.

tested for changes in (1) the number of nest boxes occupied on each plot, and (2) the maximum number of individuals counted on each plot. I used Kruskal-Wallis tests (MINITAB, Inc. 1996) to compare the heights of successful and unsuccessful nest sites and multivariate analysis-of-variance (MANOVA) tests to compare microhabitat variables around nest sites. Variables recorded as percentages were $(x + 1)^{0.5}$ transformed before analyses.

RESULTS

Nesting success.—During two breeding seasons, I monitored a total of 59 Great Crested Flycatcher nests: 32 in nest boxes and 27 in tree cavities. Most tree nests were in snags in cavities excavated by Red-bellied Woodpeckers (*Melanerpes carolinus*) or Northern Flickers (*Colaptes auratus*), but six (21%) were in natural hollows or crevices in living trees.

Twenty-four of fifty-nine nests (41%) produced ≥1 fledgling. Overall Mayfield nesting success was nearly identical between nest boxes (0.37 ± 0.05 SE) and tree cavity nests (0.38 ± 0.06 SE; $Z = 0.22$, $P = 0.41$). However, annual nesting success was higher in nest boxes (0.53 ± 0.06 SE) than in cavities (0.33 ± 0.10 SE) during 1997 ($Z = 1.77$, $P = 0.039$) and lower in nest boxes (0.26 ± 0.07 SE) than in cavities (0.42 ± 0.09 SE) during 1998 ($Z = 1.42$, $P = 0.078$). Whereas nesting success in tree cavities did not differ significantly between years ($Z = 0.64$, $P = 0.26$), nesting success in nest boxes dropped from 53% during the first year to only 26% during the second year ($P = 0.001$) because of lower nest success during incubation (Table 1). I was unable to continue the experiment for additional years because of extensive tree cutting in several nest box plots during 1999–2000.

Six of the nest boxes used by Great Crested Flycatchers during 1998 had been used previously (five in 1997, one in 1998) either by conspecifics or by Tufted Titmice. Only one of these six nests (17%) was successful, while 5 of the 14 (36%) nests in previously unused nest boxes were successful.

Nest predators.—Nest predation was the most common cause of nest failure, accounting for at least 29 of 35 (83%) nest failures. Three nests failed due to abandonment (two in nest boxes during 1997, one in a snag during 1998). Cause of nest failure was undetermined for three nests in high tree cavities during 1997.

Flying squirrels preyed on three Great Crested Flycatcher nests during the incubation period. In each case, the eggs were broken or missing, the nest was in disarray, and flying squirrels were observed on top of the nest. In addition, many depredated nests in nest boxes were disturbed in a similar fashion during the incubation period but squirrels were not observed subsequently. Corn snakes preyed on two flycatcher nests, one containing five 12-day-old nestlings and the other containing three 13-day-old nestlings; in each case, the snake remained in the nest box for ≥2 days after consuming the nestlings. Although yellow rat snakes were not observed preying on Great Crested Flycatcher nestlings during the study, they did prey on Red-bellied Woodpecker nestlings in the study area (pers. obs.).

Twenty percent of all nest boxes were occupied by flying squirrels as primary roost sites, but I found no evidence that local squirrel populations increased during the study. Maximum number of flying squirrels counted in each plot during the peak Great Crested Flycatcher nesting season (mid-April through May) did not differ significantly between years (Wilcoxon signed rank test, $S = -4.0$, $P = 0.63$). The number of nest boxes occupied by flying squirrels as primary roost sites during spring and summer also did not differ

significantly between years (Wilcoxon signed rank test, S = −6.5, $P = 0.33$).

Nest-site characteristics.—High and low nest boxes were used by Great Crested Flycatchers in similar proportions during 1997 and 1998 (Fisher's exact test, $P = 1.00$). The ratio of successful to unsuccessful nests did not differ significantly between high and low nest boxes (Fisher's exact test, $P = 1.00$). Height of tree cavity nests did not differ significantly between years (Kruskal-Wallis test, $H = 0.57$, df = 1, $P = 0.45$) or between successful and unsuccessful nests (Kruskal-Wallis test, $H = 0.65$, df = 1, $P = 0.42$). Habitat characteristics around nest sites did not differ significantly between nest boxes and tree cavities (MANOVA, Wilks Lambda = 0.650, $P = 0.35$) or between years (MANOVA, Wilks Lambda = 0.708, $P = 0.43$).

DISCUSSION

This study documented high rates of nest predation in nest boxes. Although nesting success in tree cavities did not differ significantly between years, nesting success in nest boxes was less during the second year because of increased predation during the incubation period (Table 1).

Nest predators.—Direct evidence of nest predation by flying squirrels was found only during the incubation period. Although other researchers have inferred flying squirrel predation on Great Crested Flycatcher nests based on circumstantial evidence collected at 1-week intervals (Taylor and Kershner 1991, White and Seginak 2000), this study confirmed flying squirrel predation on eggs at three nest boxes. Flying squirrels have been reported preying on eggs of other cavity-nesting birds, including Black-capped Chickadees (*Poecile atricapillus*; Stabb et al. 1989) and Red-cockaded Woodpeckers (*Picoides borealis*; R. N. Connor pers. comm., J. J. Kappes pers. comm.). Direct evidence of nest predation by snakes was found only during the nestling period. Snakes generally prey on cavity nests during the nestling period and not during incubation (Laskey 1946; Jackson 1970, 1977; Hensley and Smith 1986; Eichholz and Koenig 1992). Together, these data suggest that snakes were not primarily responsible for the high level of egg predation in nest boxes during the second year of the study.

Nest predator densities.—I assessed whether the availability of nest boxes could have increased local densities of flying squirrels, thereby increasing the odds of a squirrel opportunistically encountering and raiding a flycatcher nest. Both the total number of flying squirrels using nest boxes and the number of nest boxes occupied by one or more squirrels did not change between years, indicating no increase in the movement of squirrels among nest boxes during 1998.

Potential for learning by nest predators.—Several researchers have demonstrated a positive correlation between the risk of nest predation and the age of a nest site, both within (Nilsson et al. 1991) and across (Martin and Li 1992, Martin 1993) cavity-nesting bird species; species and individuals that excavate new nest cavities have lower rates of nest predation than do nonexcavators that rely on old cavities for nest sites. One explanation for this pattern is that nest predators may be more cognizant of locations of older nest sites. Robertson and Rendell (1990) found that nesting success of Tree Swallows (*Tachycineta bicolor*) in nest boxes decreased over time because of increasing predation by raccoons (*Procyon lotor*) and rat snakes. Sonerud (1985a, 1985b, 1989) demonstrated experimentally that pine martens (*Martes foina*) developed long term spatial memory of the locations of nest boxes used by Boreal Owls (*Aegolius funereus*). In Sweden, nest boxes for Common Goldeneyes (*Bucephala clangula*) that were preyed upon in a given year also tended to be preyed upon in successive years (Dow and Fredga 1983).

In this study, predation on eggs in nest boxes increased markedly during the second year of the study. Nest success was highest in new nest boxes (i.e., 1–2 months after installation in 1997) than in older nest boxes or in cavities. Nests in boxes that were reused for a second time were more likely to fail than nests in boxes being used for the first time. Moreover, predation rates on artificial nests placed in nest boxes (after the conclusion of this study) were higher in nest boxes that had been used previously by Great Crested Flycatchers than in nest boxes that had no previous nesting attempts (unpubl. data). These results suggest that nest predators in this study learned to exploit nest boxes as a prey resource, either

through the development of long term spatial memory or search images.

Using cameras, Farnsworth and Simons (2000) documented flying squirrels and snakes returning to depredated Wood Thrush (*Hylocichla mustelina*) nests several days after the original predation event. Such observations suggest that a variety of nest predators are capable of learning the locations of profitable prey sites and returning periodically to them. Although flying squirrels probably were responsible for most predation on eggs during 1998, snakes also may have played a role. Taylor and Kershner (1991) observed a small (56-cm) rat snake taking a Great Crested Flycatcher nestling from a nest box 2 days after another nestling had disappeared from the same nest box; they speculated that the snake made return visits because of its relatively small size.

Nest-site characteristics.—Nest boxes and tree cavity nests did not differ significantly in any habitat variable that would influence nest concealment, nor did these variables differ significantly between years. This is perhaps not surprising, given the even-aged, relatively homogeneous structure of the pine plantations. Heights of successful and unsuccessful nests did not differ significantly for nest boxes and cavity nests in either year. Thus, lower nest success in nest boxes cannot be attributed to a difference in the accessibility of these sites to predators, either between nest sites or between years. It is unknown whether nest boxes were more conspicuous than tree cavities because they were mounted externally on the tree trunk, whereas cavities are contained within the tree bole.

Physical dimensions of the nest cavity also did not appear to be responsible for predation differences. Most tree cavities used by Great Crested Flycatchers were old Red-bellied Woodpecker cavities, whose openings range from 5.0–5.7 cm in diameter (Jackson 1976, Shackelford et al. 2000, unpubl. data). Entrances at nest boxes (5.1 cm diameter) were no larger or more accessible than tree cavity nests. Obviously, temporal differences in nest predation in nest boxes were not influenced by cavity entrance size because all nest boxes had the same size entrance hole.

Ectoparasite loads, although not measured, could not have accounted for lower nest success in nest boxes during the second year, because (1) nest boxes were thoroughly cleaned of nesting debris during the intervening winter, and (2) the majority of nest failure occurred because of predation on eggs.

Conclusions.—This study demonstrates that nest boxes are not always safer sites than tree cavities. My results also underscore the importance of looking at temporal dynamics of nest predation, as static comparisons of nest success between natural sites and nest boxes may give incomplete or misleading results. If years were pooled in this study, then one would have concluded that Great Crested Flycatchers had nearly identical nesting success in nest boxes and tree cavities. Many researchers do not report annual differences in nest success and/or nest predation in nest boxes (e.g., Korpimäki 1984, Nilsson 1984, Kuitunen and Aleknonis 1992, Purcell et al. 1997). Other researchers present evidence that nest predation increases over time in nest boxes without discussing the ecological significance of this pattern (e.g., Bellrose et al. 1964, Dugger et al. 1999). When researchers undertake comparisons of breeding ecology in nest boxes and tree cavities, it is important that they report annual changes in these parameters.

Theoretical and empirical evidence indicates that nest predation may increase with the age of a nest box. The predictable, permanent locations of nest boxes may make them more vulnerable than tree cavities to nest predators over the long term (Sonerud 1985a, 1985b, 1989, 1993). Further research is needed to identify the factors—including type of predators (mammal, snake, bird), availability of alternative prey in the study area, persistence times of natural nest cavities in the study area—that determine how predators respond to nest boxes. For example, predation by martens on Boreal Owl nests appears to be influenced by the abundance of alternative prey; in a study area with low rates of nest predation (5%) and abundant microtine rodents, Korpimäki (1987) found little relationship between nest box age and predation rates by martens. I predict that, within a given area, nest predation rates will tend to be higher in nest boxes than in tree cavities if cavities in that area are relatively short-lived (i.e., they do not persist as long as the nest boxes) and nest pred-

ators in that area are sufficiently reliant on bird eggs and nestlings in their seasonal diet.

Tree cavities can vary considerably across a species' range or within a study area with respect to height, age, volume, structural integrity, accessibility to predators, and in the densities at which they occur. Nest boxes are useful tools that allow manipulation of many of these factors in controlled experiments, thus facilitating the study of particular mechanisms or ecological relationships that otherwise would be difficult or nearly impossible to study (Koenig et al. 1992). Further use of nest boxes in carefully designed experiments is warranted.

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NEST PREDATION IN FRAGMENTED FORESTS: LANDSCAPE MATRIX BY DISTANCE FROM EDGE INTERACTIONS

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ABSTRACT.—Forest fragmentation due to forestry management, agricultural activities, or urban development decreases habitat availability for some animals. This decline in forest area has been implicated in songbird population declines via changes in nest predation pressures. The increase of edge habitat that accompanies deforestation also may affect songbird breeding activities through changes in predation risk. This study found evidence for an interaction effect of distance from edge (1, 15, 30, and 45 m) and adjacent landscape matrix (residential or forested) on nest predation rates using an artificial nest design. In fragments bordered by other forested patches, nest predation rates were lowest 1 m from the edge and higher 15–45 m into the forest patch. When the forest fragment was embedded in a landscape matrix of residential and developed plots, predation rate was highest closest to the edge of the fragment. *Received 28 August 2000, accepted 13 March 2002.*

Accumulating evidence suggests that many Neotropical migrant songbirds are experiencing drastic population declines (Terborgh 1989). Forest-nesting birds are challenged by loss of breeding habitat, fragmentation of breeding habitat into smaller and smaller forest patches, and changes in the landscape surrounding these forest patches. These habitat changes can have a myriad of effects on forest nesting species (Hagan and Johnston 1992). Population density may increase immediately upon forest fragmentation, leading to increased competition for suitable nest sites and prey items (Hagan and Johnston 1992, Van Horn et al. 1995, Hagan et al. 1996, Holmes et al. 1996). Cowbird parasitism may increase (Terborgh 1989). Predator community composition may change, resulting in increased rates of nest predation (Bider 1968, Gates and Gysel 1978).

Nest predation is a major cause of reproductive failure in birds (Ricklefs 1969), and changes in nest predation rates may cause the disappearance of sensitive bird species from fragmented landscapes. Results from numerous studies consistently have demonstrated that nest predation rates increased as forest fragment size decreased (Wilcove 1985, Møller 1988, Small and Hunter 1988, Yahner and Scott 1988, Paton 1994, Hoover et al. 1995, Hartley and Hunter 1998, Keyser et al. 1998). However, it is less clear whether this effect resulted from decreased core forest area *per se* or from increased amount of edge habitat.

Edges are transitional zones from one habitat type to another. They are characterized by abiotic and biotic features distinct from the habitats on either side of the edge. For example, increased sunlight and wind exposure at edges often change the plant species composition at edges. Edge effects have been implicated in songbird population declines, and several studies have attempted to document edge effects on nest predation rates. However, the results of these studies have been contradictory (e.g., Gates and Gysel 1978, Yahner and Wright 1985, Angelstam 1986, Andrén and Angelstam 1988, Small and Hunter 1988, Møller 1989, Linder and Bollinger 1995, Hanski et al. 1996, King et al. 1996, Keyser et al. 1998). This lack of consistency may be due to problems of experimental design (Paton 1994, Murcia 1995). In many studies, the landscape matrix surrounding the forest fragments was not considered; however, the few studies that did measure nest predation relative to surrounding landscape characteristics found them to be very important (Andrén and Angelstam 1988, Andrén 1995, Donovan et al. 1997). Edge effects also may be confounded by the effect of forest fragment size. Finally, many researchers expect a monotonic relationship between distance from edge and nest predation rates. Few artificial nest studies have used nests placed at controlled distances from the edge and thus they were not capable of

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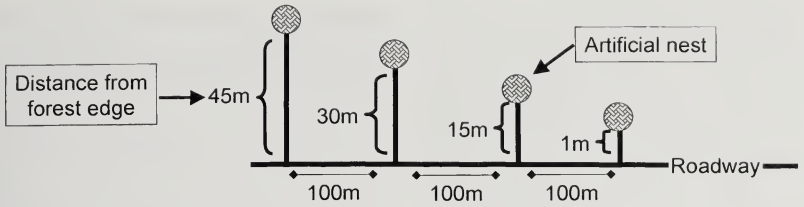

FIG. 1. Schematic of artificial nest placement, northeastern Alabama, 1997. Black lines show the path walked by the researcher when laying each nest. This protocol reduced the probability of predator trap-lining by ensuring that each nest is separated by ≥116 m of human trail.

detecting threshold edge effects at small spatial scales.

Murcia (1995) described three types of edge effects: (1) changes in abiotic conditions, (2) direct changes in abundance or distributions of particular species caused by altered abiotic conditions, and (3) indirect changes in abundance or distribution of a particular species as a result of interspecific interactions. In a previous study (Keyser et al. 1998), I suggested that changes in large predator activity (direct biotic effect of fragmentation) increased the predation pressure on songbirds in small forest fragments (indirect biotic effect). However the design of the first experiment did not permit a robust test for edge effects. The current study is designed to circumvent experimental design problems described by Murcia (1995) and Paton (1994) and provide a strong test for edge effects on nest predation rates. Specifically, I tested for an effect of surrounding landscape matrix (forested or developed edge type) and distance from edge on predation of artificial nests.

STUDY AREA AND METHODS

The study was conducted at Fort McClellan (33° 42′ N, 85° 45′ W) in northeastern Alabama at the southern end of the Appalachian region. I identified three large forest fragments (457, 586, and 849 ha; all mature mixed pine-hardwood); for detailed description see Keyser et al. (1998). Paved roads ≥10 m wide with open canopy separated these fragments. They were bordered by developed land consisting primarily of homes or administrative buildings surrounded by lawn. Thus, the study area consisted entirely of large forest fragments, which controls for confounding effects of fragment size and avoids small fragments which could be categorized as all edge (*sensu* Yahner and Wright 1985).

Two types of edge were present: (1) the border between forested and developed land and (2) the roadway border between forest fragments (hereafter referred to as residential edge and forest edge, respectively). The edge type categorized the landscape matrix in which the edge occurred and was the first treatment in this experiment. The second treatment was distance from edge. Artificial nests were placed in the forest fragment at four distances from the edge (1, 15, 30, and 45 m) in both edge types. The scale of edge effects may vary; however, the metaanalysis by Paton (1994) suggested that most edge effects probably occur ≤50 m from edge.

Each artificial nest consisted of a small (about 10 cm in diameter) scrape in the leaf litter and contained two fresh Northern Bobwhite (*Colinus virginianus*) eggs and two eggs (about 12 mm wide) made of gray Plasticine (Roma Italian Plastilina). The fresh eggs provided appropriate visual and olfactory cues to potential predators, and the artificial eggs allowed me to note when small predators, such as mice (*Peromyscus* spp.) and eastern chipmunks (*Tamias striatus*), visited the nest. Mice and chipmunks are unable to damage the relatively large bobwhite eggs (Roper 1992; Haskell 1995a, 1995b), but the use of both bobwhite and Plasticine eggs allowed me to sample effectively the activities of both large and small predators (Donovan et al. 1997, Keyser et al. 1998).

Artificial nest studies provide an index to predation pressures. They can not provide an accurate measure of predation rates on real nests because they do not simulate the nest concealment and nest defense provided by parent birds. Nonetheless, in a study such as this one, they do measure differences in predation risk among treatments.

Since each individual nest was considered an independent sample for this experiment, it was important to minimize the potential for a single predator to trapline between nests. To this end, I wore gloves while constructing artificial eggs and nests. I walked 100 m along the fragment edge before entering the fragment and walking the appropriate distance to place the nest. I then retraced my steps back to the fragment edge, when possible to a paved road, and paced out or drove another 100 m before entering the patch again to set another nest. The first nest was placed at 1 m, the second at 15 m, the third at 30 m, and the fourth at 45 m from the fragment edge, at which point, the cycle was repeated (Fig. 1). As a result, the human trail from nest to nest was ≥116 m. In total, 20 nests per distance interval were laid along the forest edge type, and 17 nests per distance interval were laid along the residen-

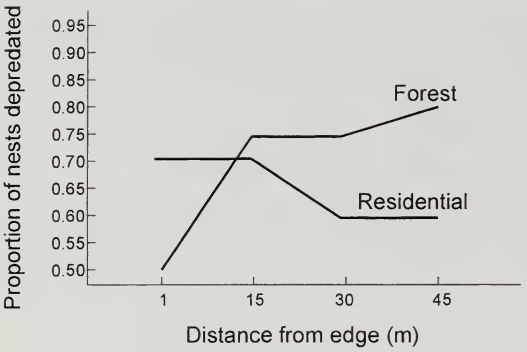

FIG. 2. The proportion of artificial nests depredated in each distance class within the two types of landscape matrix, northeastern Alabama, 1997. For the forest edge type, 10 of 20, 15 of 20, 15 of 20, and 15 of 19 nests were depredated at 1, 15, 30, and 45 m, respectively. For the residential edge type, 12 of 17, 12 of 17, 10 of 17, and 10 of 17 nests were depredated at 1, 15, 30, and 45 m, respectively.

tial edge type. The experiment was set up during the morning on 17 July 1997, and all nests were checked four days later. If any eggs in the nest were damaged, I scored the nest as depredated.

I analyzed these data in two different ways, multiple logistic regression and resampling. For the logistic regression, the response variable was binomial: either the nest was depredated or it was intact. The predictor variables include distance from edge, edge type, and an interaction term. The following model was fit:

$$\ln\left[\frac{p_i}{1 - p_i}\right] = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 (x_1 \times x_2),$$

where p_i is the probability of depredation on any given nest, x_1 is distance from edge, x_2 is edge type, and $x_1 \times x_2$ is the interaction effect (Neter et al. 1996). I used this model to test the hypothesis that predation events depended on location of the nest relative to fragment edge and landscape matrix against the null hypothesis that predation events were stochastic. Initial model fitting and calculation of Wald chi-squared statistics for parameter estimates were performed with SAS 6.09 (SAS Institute, Inc. 1998). Model fit diagnostics including the Hosmer-Lemeshow fit statistic and an index plot of deviance residuals were calculated using SPSS 10.0 (SPSS, Inc. 1999). Pearson residuals and examination of linearity of the logit for distance from edge were performed on a spreadsheet.

Graphical inspection of the data (Fig. 2) suggested that there was an interaction between distance from edge and edge type, but that the effect of distance from edge within edge type was weak. Thus, the three-parameter logistic model may not be the most appropriate way to detect the interaction effect in the absence of strong main effects. As an alternative statistical test, I used resampling to analyze the interaction between distance from edge and edge type. The resampling approach has several strengths. First, the researcher can define a test statistic that is appropriate for the particular question at hand. Second, the test is free from assumptions about the distribution of the test statistic (Manly 1997).

I calculated the test statistic in the following manner. For each combination of distance from edge and edge type (eight treatment combinations in total), I calculated the predation rate. Next, I calculated the Pearson correlation coefficient between distance from edge and predation rate for each edge type separately and then calculated the difference between the two correlation coefficients ($r_{\text{residental}} - r_{\text{forest}}$), which I refer to as the difference coefficient. To test for significance of the difference coefficient, I randomized nest fate (depredated or intact) with respect to distance from edge within each edge type and calculated the Pearson correlation coefficient for the randomized data. For example, within the forest edge type, there were 80 experimental nests, 20 per distance class. Once the nest fates were assigned randomly, there were still 20 nests per distance class, but the proportion depredated in each distance class was randomly generated. After the correlation coefficients were calculated for each edge type, I calculated the difference coefficient. This was repeated 10,000 times to generate a frequency distribution against which to compare the test statistic calculated from the real data. I performed the randomization and calculated the correlation coefficients and difference coefficients in a spreadsheet using a Visual Basic program kindly provided by Dr. D. Hoyt (program available upon request).

To determine the significance of the test statistic calculated from the actual data, I sorted the 10,000 difference coefficients calculated via randomization and noted the number of random values that exceeded the absolute value of the test statistic. This enabled me to calculate the probability that a value larger than the test statistic would be obtained through random chance.

RESULTS

Overall predation of artificial nests was high (67%, 99 of 147 nests depredated). From Plasticine eggs, I was able to identify some of the predators, and they included mice, birds, deer (*Odocoileus virginianus*) and fox or raccoons (*Procyon lotor*). However, the predator at most (59%) depredated nests was unidentifiable because both bobwhite and Plasticine eggs had been removed from the nest.

The effect of distance from edge on predation rates appeared to differ among edge types (Fig. 2). In general, predation was highest at 1 m and 15 m when the fragment was bordered by residential development. In a forested matrix, predation was lower at 1 m and higher 15–45 m within the fragment. As quan-

tified by logistic regression, the statistical significance of this pattern was not strong. Logistic regression analysis resulted in the following model:

$$\ln\left[\frac{p_i}{1 - p_i}\right] = 0.224 + 0.029x_1 + 0.712x_2 - 0.043(x_1 \times x_2).$$

The overall model was nonsignificant ($\chi^2 = 4.76$, df = 3, $P = 0.19$) as were the estimates for β_0 ($\chi^2 = 0.32$, $P = 0.57$), β_1 ($\chi^2 = 3.34$, $P = 0.068$), and β_2 ($\chi^2 = 1.41$, $P = 0.23$). However, the estimate for β_4, the coefficient for the interaction term, approached significance ($\chi^2 = 3.76$, $P = 0.053$). This suggested that the interaction effect between distance from edge and edge type may have been a more important determinant of predation patterns than simple main effects.

The results of the Hosmer and Lemeshow test showed that this analysis was appropriate for these data ($\chi^2 = 1.40$, $P = 0.97$). Using ungrouped data (all data points equal to either 0 or 1), I calculated deviance residuals and generated an index plot (Neter et al. 1996). This approach revealed no obvious outliers. Using grouped data (predation rate in each of eight distance from edge by edge type groups), I calculated Pearson residuals. When plotted against the predicted predation rate, the residual plot was ambiguous because there were only eight data points. Similarly, it was difficult to assess the linearity of the logit transformation for distance from edge because this required calculating the predation rate for each group, which reduced the sample size to four per edge type. However, I plotted the logit of predation rate, ln(p/q), against distance from edge for each edge type. Visual inspection of the plot showed no obvious deviations from linearity, although linear regression analyses were nonsignificant (forest edge: $r^2 = 0.72$, $F = 5.23$, $P = 0.15$; residential edge: $r^2 = 0.81$, $F = 8.27$, $P = 0.10$). I attributed the lack of significance to the degrees of freedom (df = 3), not to a lack of linearity.

The resampling approach was sensitive enough to detect the interaction using the difference coefficient statistic ($r_{\text{residental}} - r_{\text{forest}}$). There was a nonsignificant, negative correlation between distance from edge and predation rate in the residential edge type ($r = -0.897$, $P = 0.10$). In the forested edge type, the correlation was positive and also nonsignificant ($r = 0.835$, $P = 0.17$). The lack of significance in these two correlations was attributable to the reduction in degrees of freedom that occurred when I calculated predation rate for each distance from edge by edge type combination, but also was reflective of weak main effects as revealed by the logistic regression analysis. However, the resampling approach allowed me to document the interaction effect between distance from edge by edge type more convincingly. The difference coefficient calculated from the real data was significant when tested via resampling (difference coefficient = -1.732, $P = 0.018$). The difference coefficient quantified the difference in nest predation trend between forested and residential edge types and suggested that edge type influenced whether the relationship between distance from edge and predation rate was negative or positive. This result suggested that the interaction between distance from edge and edge type was the most meaningful biological pattern detected in the experiment.

DISCUSSION

Data from point counts conducted in my study area suggest that many Neotropical migrant songbird species no longer breed in small forest fragments (Soehren 1995). In a previous experimental study, we observed changes in predator activity with forest fragmentation and concluded that increased nest predation intensity may, in fact, be a potential cause of songbird population decline (Keyser et al. 1998). This study provides more supporting evidence. Nest predation patterns in the study area appear to be associated with distance from edge and the type of landscape surrounding the forest patch. The potential effect of forest fragmentation on nesting songbirds depends upon the interaction between these two variables. An accurate assessment of nest predation dynamics requires consideration of this interaction. It is possible that edge-related changes in predator activity or community composition are driving the pattern observed in this study. This is especially likely to be the case if predator species respond differentially to the surrounding landscape matrix.

Many previous studies have looked for

edge effects on nest predation rates in both natural and experimental designs. However, previous results have been equivocal. Paton's (1994) review of the literature found that 14 of 21 studies documented increased predation rate near edges. A metaanalysis by Söderström et al. (1998) found increased predation on nests <50 m from edge relative to nests deeper in the forest fragment. However, only about half of the studies that looked for edge effects found them. In these studies, researchers did not control for the effects of the landscape matrix in which fragments were embedded. This might explain the disparity of results.

The edge effects observed in this study would have been obscured had I not controlled for edge type. My results are consistent with a number of other studies. A review by Andrén (1995) suggested that edge effects on nest predation occurred in forest fragments embedded in an agricultural landscape but not in a forested landscape (see also Bayne and Hobson 1997). My result supports a metaanalysis by Hartley and Hunter (1998) that showed a trend toward increased edge-related predation only in deforested landscapes (both studies in deforested landscapes found edge effects, but only 3 of 13 in a forested context showed edge-related increases in predation).

A complete understanding of nest predation dynamics in ecotones depends upon many factors. Species specific habitat use, nest placement or concealment, and nest defense all can influence nest predation patterns (Pasitschniak-Arts et al. 1998, Restrepo and Gómez 1998). In addition, predator specific, edge-related predation has been shown in several studies (Pasitschniak-Arts and Messier 1996, Arango-Velez and Kattan 1997, Bayne and Hobson 1997). Understanding the behavioral patterns of nesting birds and potential predators relative to the abiotic characteristics of ecotones will facilitate a deeper understanding of edge effects.

Although the pattern was somewhat weak, my study found evidence for an interaction between distance from edge and edge type that influenced nest predation patterns on small spatial scales. Further study clearly is warranted to determine if the same pattern holds in other locations, and if so, to determine the underlying cause of differential nest predation.

ACKNOWLEDGMENTS

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BREEDING BIOLOGY OF THE BLACK-BACKED LESSER GOLDFINCH IN PONDEROSA PINE FORESTS ON THE COLORADO FRONT RANGE

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ABSTRACT.—We present information on nest site characteristics and breeding biology of the black-backed race of the Lesser Goldfinch (*Carduelis psaltria psaltria*) in montane ponderosa pine (*Pinus ponderosa*) woodland in the foothills of Boulder County, Colorado. We located 62 nests during summer, 1999–2001. There appeared to be strong microhabitat preferences for nest sites. Nests generally were placed toward tips of long branches in the middle of ponderosa pines. Most nests were well concealed in needle clusters in trees near forest edges and openings. Mean canopy cover at nest sites was 49%. Nests usually were oriented toward the south or east, and orientation was correlated with the aspect of the surrounding terrain. More than 70% of nests were located in small, loose colonies. Nesting success was fairly high; at least 21 nests fledged young while only 10 failed due to predation. Mayfield nest success was 73% during 2000 and 52% during 2001. Most predation events occurred after the eggs had hatched. We found only one instance of brood parasitism by the Brown-headed Cowbird (*Molothrus ater*). Compared to the green-backed race (*C. p. hesperophila*), Black-backed Lesser Goldfinches appear to breed later in the season and have smaller clutch sizes. *Received 13 November 2001, accepted 28 June 2002.*

Two races of the Lesser Goldfinch (*Carduelis psaltria*) occur in North America. The green-backed race (*C. p. hesperophila*) is primarily resident from southwestern Washington to Baja California and eastward through Utah, central Arizona, and Sonora (Watt and Willoughby 1999). It is a widespread breeder in California and Baja California, and occasionally farther north on the West Coast (Watt and Willoughby 1999). The black-backed race (*C. p. psaltria*) ranges from Colorado and western Oklahoma southward through Mexico to Guerrero, Oaxaca, and central Veracruz (Gross 1968, Watt and Willoughby 1999). In Colorado, it is a fairly common breeder in foothills, mesas, and plains of both the eastern and western slopes (Andrews and Righter 1992, Levad 1998). Unlike the green-backed race, this subspecies is partially migratory, withdrawing during winter from Colorado, Utah, and northern New Mexico (Watt and Willoughby 1999). However, winter sightings recently have increased in the intermountain west (Versaw 2000).

Due in part to the difficulty in locating and monitoring Lesser Goldfinch nests, little information exists on the breeding biology of this species. The few extensive studies of Lesser Goldfinch breeding biology were conducted in California, where the green-backed race is prevalent (Coutlee 1968a, 1968b; Linsdale 1968). Almost all data on the black-backed race is anecdotal (see Watt and Willoughby 1999). These subspecies differ considerably in their migratory behavior, timing of breeding, and molting pattern (Watt and Willoughby 1999), so comparative studies of other aspects of their breeding biology are of interest. During the summers of 1999, 2000, and 2001, we located and monitored nests of Black-backed Lesser Goldfinches on open space properties in and around Boulder, Colorado. We provide here information on the breeding biology and nest site selection on this relatively poorly studied subspecies.

STUDY SITES AND METHODS

Our study sites were located on city- and county-maintained open space properties in the foothills around Boulder, Colorado (40° 00′ N, 105° 16′ W; elevation 1,600–1,900 m). We located and monitored nests in 10 plots ranging from 4–6 ha in size. These plots were dominated by ponderosa pine (*Pinus ponderosa*) woodland and savannah with a mixture of Douglas fir (*Pseudotsuga menziesii*) at higher elevations. We did not search for nests in residential or riparian areas, although such areas bordered some plots. All of our plots were within a few kilometers of the

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city of Boulder and were subject to varying degrees of human disturbance.

Our field seasons extended from late May through mid-August, 1999–2001. We monitored nests at intervals of 2–4 days (normally every 3 days) following standard nest monitoring protocols (Ralph et al. 1993) until they were no longer active. We tried to limit nest failure from factors associated with nest monitoring (Martin and Geupel 1993). We determined nest contents by direct observation or by using a mirror mounted on a 6-m pole whenever possible, but some nests were too high to detect contents. We included all nests that were confirmed as being active, either by monitoring the contents or by observing the adults sitting on and/or visiting the nest with food.

After nests were no longer active, we measured habitat characteristics at each site using standardized protocols (James and Shugart 1970, Martin and Roper 1988). At the nest, we measured nest tree height, nest tree diameter (dbh), canopy cover over the nest, distance of nest to trunk and to tip of supporting branch, and the height of the lowest living branch on the nest tree. We measured distances with a measuring tape whenever possible, but heights of tall trees and higher nests were measured with a Suunto PM-5/360 PC clinometer. We measured canopy cover by obtaining a mean of four measurements with a Lemmon model-A convex spherical densiometer at a distance of 1 m from the nest in the four cardinal directions (Lemmon 1957). We measured slope and aspect of the terrain around the nest site using a compass and clinometer. Finally, we documented the location of each nest using a Garmin GPS-12 global positioning system. This made it possible to determine the distance to the nearest adjacent active Lesser Goldfinch nest for nests on sites where more than one such nest was located.

We used data from 38 nests (16 in 2000, 22 in 2001) in which the contents were determined to calculate nest success. Seven of these nests had unknown fates, mostly because they were still active at the time our field crew was disbanded and they could not be checked regularly afterwards. To calculate nesting success we followed the method proposed by Mayfield (1975), with adjustments suggested by Manolis et al. (2000) for nests of unknown fate. We used a mean egg-laying/incubation period of 14 days and nestling periods of 13 days in the calculations based on a sample of our own nests for which we had accurate data (see below).

We performed Shapiro-Wilks *W*-tests to determine whether goldfinch nests were normally distributed in their placement in relation to canopy cover, tree height, and branch length. We used a Rayleigh test (Zar 1999) to determine if there was a significant directional component to nest orientation with relation to the trunk of the nest tree. We used a Spearman correlation to determine if there was a significant relationship between aspect and the orientation of the nests. In this case both measurements were in degrees and the minimum degree distance between the two measurements was considered the difference. Finally, we used the nonparametric Wilcoxon test to determine if clutch size differed between 2000 and 2001 or between our data and that reported by Watt and Willoughby (1999) for the green-backed race. Statistical significance was set at $\alpha < 0.05$. All tests except the Rayleigh test were performed using JMP Statistical Software (SAS Institute, Inc. 1995). Means and standard deviations are provided for all measurements included in the results.

TABLE 1. Distances between active nests of Lesser Goldfinches (*Carduelis psaltria*) in four colonies located in ponderosa pine habitat near Boulder, Colorado, 2000–2001.

Colony	Year	Number of nests	Mean (±SD) distance between active nests (m)	Range (m)
A	2000	9	77 ± 44	24–124
A	2001	15	60 ± 25	26–115
B	2001	7	85 ± 26	53–113
C	2001	10	50 ± 41	17–118
All colonies		41	65 ± 36	17–124

RESULTS

All but one of the 62 nests were placed in thick clusters of needles in ponderosa pine trees. The remaining nest was placed in a branch fork of a tall Douglas fir sapling. Mean nest height was 6.1 m ± 1.7 m, and ranged from 2.2–15.0 m. Nest tree height appeared to influence placement, as mean nest height was 56% of total tree height and the distribution of nests around this mean was normal ($W = 0.98$, $P = 0.82$). Nests almost always were placed well out on long branches, with 55 of 62 nests located ≥70% of the distance out along the branch in a strongly skewed distribution ($W = 0.76$, $P < 0.001$). Most nests were well concealed in needle clusters in trees near openings or edges in the forest. Canopy cover at nest sites was normally distributed around a mean of 49% ($W = 0.93$, $P = 0.73$).

Of the nests we located, 68% (42 of 62) were oriented between 90° and 210° in a nonuniform and nonrandom distribution (mean angle = 143°, Rayleigh's $R = 2.94$, $Z = 8.49$, $P < 0.001$). Nest orientation also was significantly positively correlated with the aspect of the terrain around the nest site ($r_s = 0.30$, $P = 0.018$). In at least four cases, several goldfinch nests were located in an area of <12 ha, with nests as close as 17 m to their nearest active neighbor (Table 1). Goldfinches in these colonies regularly were seen feeding and moving together in small flocks.

Nest building and egg laying occurred from the first week of June through at least the first week of August. Using nests with known dates of laying and fledging, and those for which dates could be extrapolated from available data, we determined that the breeding season extended from 2 June through 19 August, 2000, and from 1 June through 5 September, 2001. The peak of the breeding season (≥50% of nests active) occurred between 16 June and 13 July 2000, and between 26 June and 22 July 2001. Several late nests may have been second nesting attempts following previous failures. On two occasions in late July 2001, we found female Lesser Goldfinches building nests while also feeding fledglings, indicating second broods. In both cases the new nests remained empty for several days before the first egg was laid.

Egg laying dates were from 9 June through 5 August. Females laid one egg per day for a total of 3–5 eggs. Mean clutch size was 3.55 ± 0.52 (n = 11) during 2000 and 3.93 ± 0.70 (n = 15) during 2001. Clutch sizes did not differ significantly between years (Z = 1.39, P = 0.16), though larger sample sizes might have revealed differences. Our overall mean clutch size (3.77 ± 0.65, n = 26) was significantly lower than that reported by Watt and Willoughby (1999) for the green-backed race (4.15 ± 0.46, n = 20; Z = 2.18, P = 0.021). Incubation began soon after the first egg was laid, and lasted 12–15 days (mean of 13.8 ± 1.1 days, n = 14). Consequently, young hatched sequentially, usually over a period of 2–3 days. Nestlings remained in the nest another 11–15 days after the initial egg hatched (mean of 13.3 ± 1.5 days, n = 13), fledging as a group.

During the period when a nest held eggs or younger nestlings, nest attentiveness by female goldfinches was very high. On nests with known contents, we found females on their nest during 112 of 121 (93%) checks during incubation and 31 of 46 (67%) checks during the first 6 days of the nestling period. Male goldfinches regularly fed the female and/or the nestlings during these periods. After day 6 of the brooding period, females were found on the nest during only 9 of 45 (20%) checks, and both adults regularly were seen feeding the nestlings.

At least 21 Lesser Goldfinch nests successfully fledged young, while only 10 nests definitely failed due to predation. Assuming a nesting cycle of 27 days (14 days incubation plus 13 days brooding), we determined Mayfield nest success to be 73.6% during 1999/2000 and 52.1% during 2001. Mean number of fledglings produced per successful nest was 2.93 ± 0.70 (n = 21). Eight of the ten nests that failed due to predation were lost after the eggs had hatched. Only one nest was parasitized by a Brown-headed Cowbird (*Molothrus ater*).

DISCUSSION

Lesser Goldfinches nest sites in our study area were significantly correlated with some measured microhabitat characteristics. Nests usually were placed well toward the tips of branches in the midportion of ponderosa pines. Nests were well concealed in needle clusters with mean canopy cover almost 50% at the nest site. Lesser Goldfinches tended to select sites oriented to the south and east of the main trunk of the nesting tree and orientation was positively correlated with aspect at the nest site. The direction of orientation may, therefore, be related to temperature or incident sunlight. We suggest that the above characteristics may be important with respect to nest placement, at least in coniferous woodlands. Further study of the thermal characteristics of the nest and nest site selection in Lesser Goldfinches is warranted.

We found mean clutch size for Black-backed Lesser Goldfinches to be lower than that reported for the green-backed race by Watt and Willoughby (1999). However, samples sizes from both studies are small and each was taken largely from a single location and a limited number of breeding seasons. Thus, there may be considerable undocumented temporal or geographical variation in clutch size due to climate, habitat, or territory quality (Cody 1965, Ricklefs 1980, Hogstedt 1985, Kulesza 1990). Indeed, in our study we found 5-egg clutches only during 2001, when mean clutch size was higher.

Our results suggest that Lesser Goldfinch reproductive success is high, with a mean Mayfield nest success rate of 62.3% over the 3 years of the study. These values were higher than any other species on our sites for which we have a large sample size (e.g., Western

Tanager, *Piranga ludoviciana*, Fischer et al. in press; Plumbeous Vireo, *Vireo plumbeus*, Chace and Cruz 1999). This may be because Lesser Goldfinches show relatively high levels of nest attentiveness. Lesser Goldfinch females remain on the nest almost continuously from the start of incubation until after the young have hatched, apparently being fed primarily by the male during this period (Watt and Willoughby 1999; JWP and LMM pers. obs.). Most of the nests that failed were lost after this period of high nest attentiveness, supporting this conclusion. Furthermore, the well-concealed nests may deter predation. We had difficulty observing some nests, even when we knew their location.

We located only one Lesser Goldfinch nest that had been subject to brood parasitism, and few records apparently exist in the literature (Woods 1930, Chace and Cruz 1996). Lesser Goldfinches, like other small finches, probably are poor host species for cowbirds since the main portion of their diet appears to be seeds and grains (Linsdale 1957, Watt and Willoughby 1999). Middleton (1977) found 22 of 234 (9.4%) American Goldfinch (*Carduelis tristis*) nests parasitized by cowbirds in Wisconsin, but found that very few cowbird eggs hatched and no cowbird young fledged from these nests, further suggesting that goldfinches are poor hosts for cowbird parasitism. Finally, the nest attentiveness described above may serve as a deterrent to cowbird parasitism.

The Lesser Goldfinch is reported to be highly gregarious during the nonbreeding season, but less so while nesting (Watt and Willoughby 1999), despite previous reports of multiple pairs nesting in small areas (Jensen 1923, Gross 1968). While we found some individual nests, at least 41 of the pairs we studied during 2000 and 2001 were nesting in colonies (Table 1), a behavior also noted in the green-backed race (Coutlee 1968a, Watt and Willoughby 1999). The closest active nests were located ≤30 m of each other in these colonies, although mean distance between nests was about 65 m (Table 1). There was a great deal of interaction among pairs within a colony, particularly during the nest-building period and after the young fledged. While chasing and other aggressive encounters did occur, Lesser Goldfinches were seen moving and foraging together in small groups throughout the breeding period. We did not find any evidence to suggest the clustering of nests was related to dependence on water and their resulting occupation of similar habitat near one another as suggested by Gross (1968). In fact, our largest study site, which contained 9 nests during 2000 and 15 during 2001, was >2 km from any permanent water source, and the only water present in any of our sites was in the form of small intermittent streams and pools.

The timing of the breeding season, as well as the molting pattern, differs between the races of the Lesser Goldfinch (Watt and Willoughby 1999). Green-backed Lesser Goldfinches breed from April through early July in California, with a peak between mid-May and mid-June (Coutlee 1968a, Watt and Willoughby 1999). Our data, and that of the Colorado Breeding Bird Atlas (Levad 1998), suggest that Black-backed Lesser Goldfinches in Colorado begin breeding almost 2 months later, and the peak of the breeding season extends from mid-June through mid-July. As suggested by Watt and Willoughby (1999), the molting patterns of these two races probably differ due to this difference in timing of breeding. The black-backed race has time to undergo a complete prealternate molt during spring before breeding begins, while the early breeding green-backed race has no more than a limited partial molt during spring.

The results of our study reveal interesting patterns in the breeding biology of the Black-backed Lesser Goldfinch. The breeding biology of this subspecies differs in several ways from the better-studied green-backed race, which might help explain other differences between them, such as the timing of molt. Our data on nest site selection, nest attentiveness, and coloniality suggest that additional studies focused on these subjects might yield additional interesting results.

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REPRODUCTIVE BEHAVIOR AND COMMUNICATION IN BLUE-THROATED HUMMINGBIRDS

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ABSTRACT.—Previous studies of Blue-throated Hummingbirds (*Lampornis clemenciae*) showed that males have elaborate songs and females also sing. Here we report complex territorial systems, sexual behavior, and communicatory repertoires of both sexes. Males typically defended territories along streams throughout the reproductive season. Time budgets revealed that males allocated more time to vocalizing in territorial advertisement than in more energetically costly activities such as chases. Both observations and playback experiments indicated that two vocalizations have different roles in territorial advertisement. Strings of chips served in long distance territorial advertisement, while the lower amplitude song, more prevalent early in the season, attracted females and also repelled males from the immediate area. Agonistic interactions included long chases, some with vocalizations. During close range encounters an array of postures and sounds occurred. Females defended territories against other females during a brief period preceding egg laying. Sexual interactions were unusually intricate, consisting of a series of activities in which the female played an active role. She delivered loud calls advertising sexual readiness and performed aerial displays. Males competed with other males for access to females. We observed four presumed copulations, all preceded by a song fragment from the male. The vocal repertoire included at least 16 different sounds, all with different functions, an unusually large number for a nonoscine. Male songs were the most complex sounds. Behaviors that differed from many other hummingbirds that have been studied included strong reliance on vocal signals, lack of male aerial displays, and female advertisement of sexual readiness. These attributes may be linked to reduced sexual dichromatism and related to the species' preference for wooded riparian habitats. *Received 15 May 2001, accepted 2 April 2002.*

Hummingbirds provide a fascinating and difficult challenge for behavioral ecologists. The family Trochilidae includes >300 species occupying a variety of habitats (Schuchmann 1999). Although subjects of numerous ecological and physiological studies, the reproductive behavior of relatively few species has been assessed in detail, which is not surprising considering their general tropical distribution and the difficulty of studying such rapidly moving small birds. The general picture of hummingbirds that has emerged is the conservative nature of some behavior patterns and the diversity of others (Johnsgard 1997, Schuchmann 1999). Mating systems are polygynous, and males have no role in parental care, yet other behaviors vary according to the species. For example, elaborate aerial courtship displays are performed by males of many species, but are absent in others (Wagner 1954, Johnsgard 1997). Males of some species congregate in leks during the breeding season (Johnsgard 1997).

Detailed studies of visual and vocal signaling in reproductive interactions are lacking for most hummingbird species with the exception of comprehensive studies of courtship and aggression in Streamertails, *Trochilus polytmus* (Schuchmann 1980) and Anna's Hummingbird, *Calypte anna* (Stiles 1982). The monograph on ecological and evolutionary aspects of the lek mating system of Long-tailed Hermits (*Phaethornis superciliosus*) includes a description of the communicatory repertoire involved in reproduction (Stiles and Wolf 1979). Our present study is an initial contribution in assessing the nature and variety of hummingbird behavior.

The main focus of this study is visual and vocal signaling systems and their role in mediating territorial interactions and sexual behavior in Blue-throated Hummingbirds (*Lampornis clemenciae*). We document and discuss some previously undescribed behavior of this species that contributes new perspectives for integrating the role of intersexual communication in reproduction. Most studies of hum-

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mingbird reproductive behavior have focused almost exclusively on males, as they are much easier to observe because of brighter plumage and more conspicuous behavior. The marked sexual dichromatism of many species indicates that female choice may select for plumage and behavioral attributes. Vocal signals have received less attention. Here we suggest females have an active role in initiating sexual behavior, as may be the case in other hummingbird species as well.

The Blue-throated Hummingbird has an extensive range in Mexico but breeds in only a few localities of the southwestern United States where males typically defend territories along streams in montane regions from their arrival following migration (typically April) until departure in late summer (Williamson 2000). Eight male territories were spaced at uneven distances along 1,500 m of stream in Arizona (Williamson 2000). Territory size and structure are variable and related to the distribution of nectar supplies (Lyon 1976; DRP unpubl. data), but since birds also are breeding during their time in the southwestern United States, the functional importance of male territories probably extends beyond simple energy acquisition to include a staging ground for displays and vocalizations (Powers 1987).

The sexes are spatially segregated during most of the reproductive period, with only a brief overlap during sexual activity (Wagner 1952; MSF unpubl. data). Blue-throated Hummingbirds are unusual in having a more protracted period of association of the sexes than other hummingbirds studied in Mexico by Wagner (1954). Females defend two kinds of territories, with no temporal overlap: the immediate nesting area for a few days before egg laying (Wagner 1952), and temporary feeding territories later in the season (Lyon 1976).

Our previous studies described the structure and usage of complex male songs (Ficken et al. 2000). These songs comprised clusters of notes (termed "units") that we designated A, B, C, D, and E. Our initial observations indicated they may serve as short range territorial advertisement as well as female attraction. Other vocalizations, particularly strings of chips (the loud "*seeps*" of Marshall 1957), also are associated with reproductive behavior (Williamson 2000). Here we address questions concerning the different functions of songs and chips utilizing playback experiments. Using a time budget analysis, we documented the number of these two types of male vocalizations as compared with chases and other aerial territorial behavior. We also tested the prediction that longer songs should predominate earlier in the season when sexual activity is highest, if a principal function is the attraction of females. Females also utter complex muted songs, typically when close to a male (Ficken et al. 2000), and we played back these songs to males. We describe usage of a female call (designated *Tia* following its description by Wagner 1952) and supplement observations with playbacks. In addition, we describe a variety of visual signals by both sexes, some with complex components that are important constituents of reproductive behavior.

In addition to studies of general reproductive behavior and some visual displays, we provide the first sonagraphic analysis of the acoustic repertoire of a hummingbird and compare the behavior of Blue-throated Hummingbirds with some other avian species regarding acoustic repertoire categories and characteristics.

METHODS

We conducted the study from 1995–2001, with the most intensive data collection during May, and some additional observations during late April and August at two sites in southeastern Arizona (Cochise Co.): Ramsey Canyon in the Huachuca Mountains (31° 50′ N, 109° 10′ W), and the Southwestern Research Station in the Chiricahua Mountains (31° 26′ N, 110° 19′ W). Both sites had numerous feeders visited by a variety of hummingbird species. Although many observations were made <10 m from feeders, others were made at a greater distance. Some behavior was much easier to observe near feeders, because the interaction rate was increased by competition for access to feeders. Feeders undoubtedly affected many aspects of reproductive behavior, such as nest site selection and population density, but we were unable to assess all these effects. We described different types of agonistic interactions, but because of the rapidity of certain types of encounters we were not always able to describe all components for both participants.

We determined time budgets for nine males at the Southwestern Research Station and two males at Ramsey Canyon that had established territories around feeders (June to July 1995). We quantified two 30-min periods for each individual, one during the morning (09:00–12:00 MST) and one during the afternoon (12:00–17:00). The observer was positioned about 20 m from the feeder being defended by the focal male. We recorded behaviors related to territorial defense. We

divided these agonistic encounters into three major categories (chases, crouches, and hovers) for analysis of their association with vocalizations. Tail spreading and sounds often accompanied these behavior patterns. We analyzed a sequence of activities of one encounter in slow motion from a published videotape (Nature Science Network, Inc. 1988).

We recorded vocalizations and notes using Sony Professional Walkman WM-D6C cassette tape recorders and either a Nakamichi directional microphone or an Audiotechnica AT 877 microphone. Some natural behavior and many playbacks were videotaped using a Sony camcorder. We made sonograms with a Kay 7800 Sona-graph at 8 kHz with a 150-Hz bandwidth filter. For measurements of chips and *Tias,* we used Avisoft SONAGRAPH Pro (ver. 2.5).

We conducted playback experiments with the Sony Professional Walkman and a Sony SRS-27 speaker affixed about 2 m high to a branch in areas near feeders. The feeders were >50 m apart, increasing the probability that different individuals were tested.

To test whether responses differed for certain vocalizations associated with reproductive behavior, we conducted playbacks during May 1998 and May and early June 1999. We completed 14 experiments at two sites (five males at Ramsey Canyon and nine males at Southwestern Research Station). Each presumably was a different male, based on distance between playback sites. Each experiment consisted of three randomized series of vocalizations, each lasting 85 s with a 90 s interval between playbacks. Playback durations were similar to normal singing in bouts. In natural singing, a bout began with the first song and terminated when the bird ceased singing or flew. The amplitude for all playback sounds was adjusted to 70–75 dB (measured with a Yu Fung YF-20 sound level meter). For male song (Type 1 of Ficken et al. 2000), we used a common variant consisting of a string of six units (ABCDEB) repeated 11 times. Playback of female song (Type 2 of Ficken et al. 2000) lasted 1.9 s and was presented nine times, and chips were a continuous series (Serial Chips) using natural intervals. All males in the population used the same song variants, and chips were very stereotyped. Response measures for hummingbirds were necessarily different than those for oscines because of the behavioral differences between the two groups. Hummingbirds rarely perched near a speaker during playback and vocalized only infrequently. We started playbacks when a male was ≤15 m of the speaker. Responses included (1) no approach; (2) obvious movement away when playback started; and (3) approach to <10 m of the speaker, usually involving rapid agitated flights and hovering near the speaker. We noted the actions of the birds before playback, during pauses between playbacks, and after playback. For the analysis we used only behavior during playback.

In a separate set of experiments (June 1999) at the Southwestern Research Station we played *Tia* calls in areas where females had been observed producing these calls. These experiments were designed to test whether both males and females responded by approaching the speaker.

TABLE 1. Time budgets indicate that male Blue-throated Hummingbirds (*Lampornis clemenciae*) spent more time vocalizing in territorial advertisement and defense than in active aggression (chases and other nonvocal behaviors). Values are mean number of acts per 30-min observation period for individually identifiable males. Data are from the Southwestern Research Station (birds 1–9) and Ramsey Canyon (birds 10–11), southeastern Arizona, June and July 1995.

Bird	Aggressive acts	Chipping	Singing
1	0.36	18.03	0.93
2	0.00	0.53	2.04
3	0.23	7.92	0.87
4	0.65	0.28	0.45
5	0.28	17.83	1.78
6	0.58	0.57	1.04
7	0.05	9.28	0.23
8	0.94	13.12	0.39
9	0.11	22.13	0.13
10	0.17	15.50	1.07
11	0.43	0.40	0.07
Grand mean	0.35	9.60	0.82
(SD)	(0.29)	(8.25)	(0.65)

We measured sonagrams for comparisons of calls. Because of the extremely varied usage, we analyzed chips separately according to sex and context. Values are presented as means ± SD. Unless indicated otherwise, *t*-tests are two-tailed. For comparisons of responses to sound playback we used the sign test, comparing approaches during playback to the nonplayback situation. *P* values <0.05 were considered significant. The data in Tables 2 and 3 are based on ≥8 males and ≥3 females. We compared the incidence of male and female agonistic behavior patterns, but because the data were not obtained from known individuals, they only suggest trends and statistical tests were not performed.

RESULTS

Territorial behavior and time budgets related to aggression.—Time budgets undoubtedly were affected by feeders, but a major trend was clear under these conditions. Males spent more time vocalizing than engaged in overt aggression. Two males spent almost the same amount of time chipping (Serial Chips) as engaged in aggressive acts, but all the others spent much more time chipping (Table 1). Similarly, singing occupied more time for 8 of the 11 males than overt aggression. Most birds (8 of 11) spent more time chipping than singing.

There may be a relationship between territory size (and possibly quality) and degree of aggression exhibited by the territory holder. The most dominant male in our study (bird 1; Table 1) defended a large territory that appeared to be about 10,000 m^2 in size. When bird 1 was removed, his territory was broken into several smaller pieces defended by males exhibiting less dominant behavior. Another male (bird 2) who defended a territory adjacent to a dry creek encountered substantially fewer intruders and exhibited no aggressive behavior during observations (Table 1).

Male song.—Song length was related to the stage of the breeding cycle, with shorter songs more prevalent later in the season (one-tailed $t = 1.8$, df = 286, $P = 0.037$). During May songs had a mean of 4.99 ± 3.46 units ($n = 242$ songs), and during July a mean of 4.09 ± 2.75 ($n = 46$). Although some long songs persisted throughout the summer, the short song of just two units (AB) was the most common song variant, and as the season progressed the proportion of AB songs increased (18% of all songs early in the season, 33% later).

Although single songs were frequent, songs also were performed in bouts. Pauses between bouts always were much longer than intervals between songs within a bout. The longest bout was 18 songs, but most bouts were composed of only a few songs. Early in the breeding season bouts were somewhat longer (mean = 4.3 ± 3.8 songs, $n = 59$) than later in the season (mean = 2.8 ± 1.4 songs, $n = 17$; one-tailed $t = 1.6$, df = 74, $P = 0.045$).

Single Chips.—Males often were silent when perched on their territories, unless another male Blue-throated Hummingbird or Magnificent Hummingbird (*Eugenes fulgens*) approached. The other hummingbird usually left the vicinity following one or two chips by the resident Blue-throated Hummingbird. These Single Chips also preceded flight, or were uttered as the bird approached a feeder. Females usually were silent both in the vicinity of feeders and when perched away from feeders (<1% of chips we recorded were from females).

Single Chips were very short, high pitched notes (Fig. 1a). No significant differences occurred between the sexes with respect to the mean low frequency of the chips ($t = 0.99$, df = 28, $P = 0.36$) or the mean high frequency ($t = 0.99$, df = 28, $P = 0.33$), but we detected tonal differences between the sexes. Male chips sounded harsher, perhaps due to more high frequency bands than those of females, with the inclusion of a second band from 10.9–12.2 kHz (present in all 16 samples), and sometimes a third even higher band 15.9–18 kHz (present in 6 of 16 samples). We observed less banding in females, with a second band of 11.6–13.4 kHz (present in 7 of 14 samples) and no third band ($n = 14$). The most striking difference, however, was that female Single Chips were about half the duration of male Single Chips (Table 2).

Serial Chips.—Males delivered long strings of chips, particularly in the early morning and late evening, and less frequently at other times of day. Calling was most prevalent early in the breeding season. A single male called for 20 min on one occasion, and many bouts were as long as 10 min. The mean rate was 7.21 ± 1.37 ($n = 23$), and the chips were delivered at uniform intervals. Single Chips and Serial Chips did not differ significantly in frequency ($t = 1.96$, df = 32, $P = 0.058$), but individual chips in a series were shorter than male Single Chips ($t = 6.2$, df = 30, $P < 0.0001$).

Males typically perched near the creek on high perches. Serial Chipping often was accompanied by head movements (Wagner 1954; MSF pers. obs.) through an arc of about 150°. While chipping, the male occasionally altered the pitch of the call (Willard 1911), as indicated in Fig. 2. To our ears, the pitch shift and the changing amplitude during head movements produced a "stereo" effect. In fact, we believed two birds were calling when we first noted this behavior.

Female Serial Chips were rare, and all five cases occurred when a female was in the last stages of nest construction. During this time females engaged in territorial interactions with neighboring females. Female Serial Chips were associated with a head tossing movement, but unlike the males, we detected no pitch shifts in females. In females, individual chips in a series were longer than Single Chips ($t = 3.15$, df = 30, $P = 0.004$), in contrast to males.

Playback experiments of Serial Chips and male and female song.—Males responded significantly with approaches to male song (sign

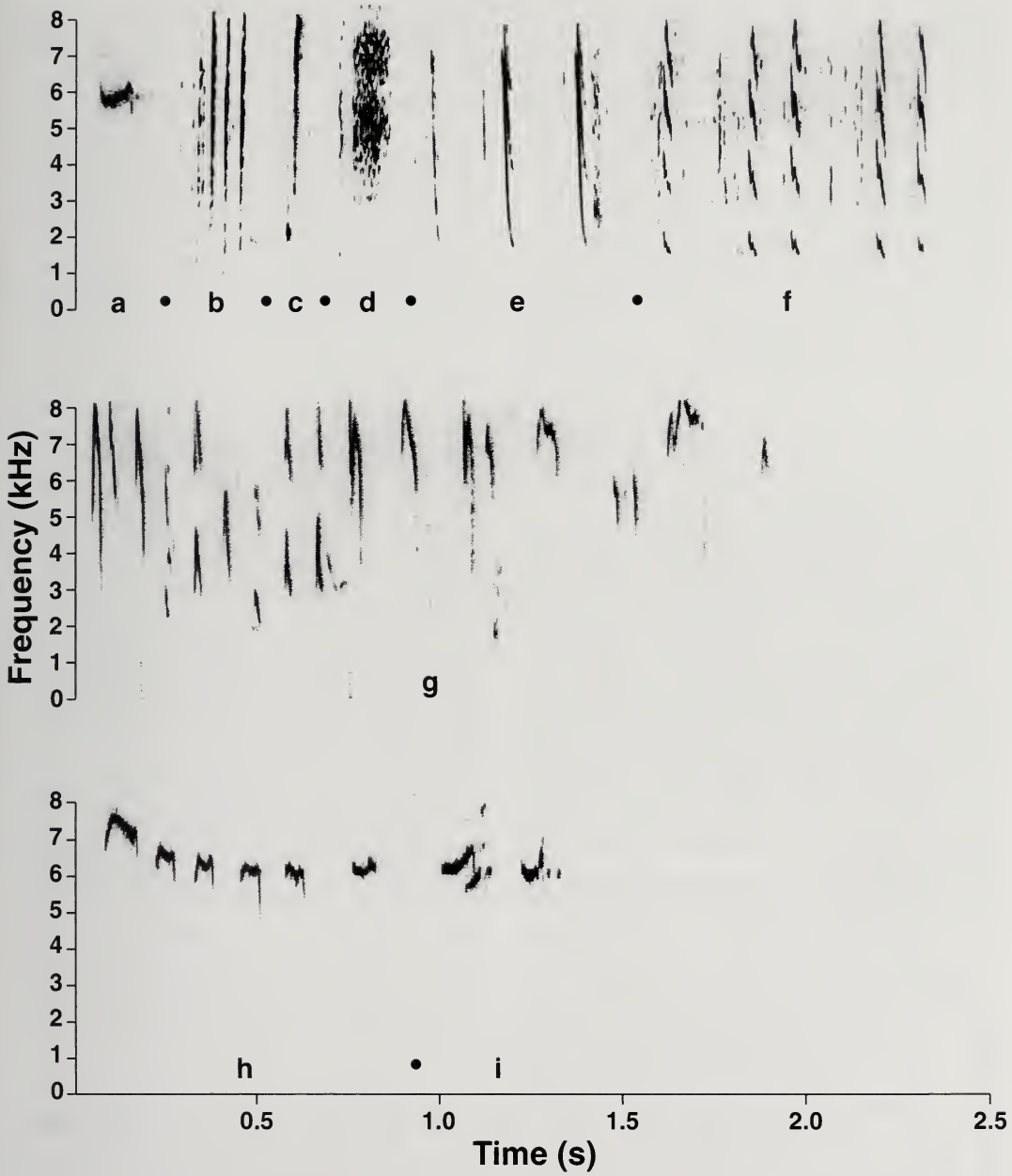

FIG. 1. Sonograms of Blue-throated Hummingbird (*Lampornis clemenciae*) vocalizations recorded at the Southwestern Research Station, southeastern Arizona, by M. S. Ficken, April through August, 1995–2001. Black circles on horizontal axis separate different kinds of calls. Sonograms were prepared using a Kay 7800 Sona-Graph with 0–8 kHz settings and a 150-Hz bandwidth. In a few cases, some elements were higher than 8 kHz. (a) Single Chip of a male. (b) Staccato Trill. (c) Bill Crack. (d) *Zeet.* (e) Short Call. (f) Long Call (most common form). (g) Complex Long Call. (h) *Tia.* (i) Mobbing Chips (more than one individual is calling).

TABLE 2. Acoustic characteristics of Blue-throated Hummingbird (*Lampornis clemenciae*) chips illustrate the variation associated with sex, age, and context. Values are means ± SD (*n*). Data are from the Southwestern Research Station, southeastern Arizona, May through June, 1995–1999.

	Duration (s)	Lowest frequency (kHz)	Highest frequency[a] (kHz)
Single chips (female)	0.11 ± 0.05 (14)	5.64 ± 0.35 (14)	6.79 ± 0.33 (14)
Single chips (male)	0.21 ± 0.05 (16)	5.50 ± 0.50 (16)	6.90 ± 0.28 (16)
Mobbing chips	0.08 ± 0.02 (23)	5.68 ± 0.21 (9)	7.63 ± 0.80 (9)
Fledgling chips	0.11 ± 0.02 (10)	7.86 ± 0.15 (9)	9.39 ± 0.17 (9)
Series chips (female)[b]	0.16 ± 0.04 (18)	5.14 ± 0.17 (11)	6.35 ± 0.14 (11)
Series chips (male)	0.13 ± 0.02 (18)[c]	5.31–6.20 (18)[d]	6.44–7.10 (18)[d]

[a] Energy distribution is centered in this band.
[b] Mean of means for two female chip series.
[c] Mean of means for five male chip series.
[d] Mean of ranges for five male chip series, depicting the pitch shift for these vocalizations.

test, $L = 1$, $n = 14$, $P = 0.002$), but only two approaches by males occurred during playback of female song ($L = 2$, $n = 14$, $P = 0.012$). Responses to playbacks of Serial Chips were ambiguous, with two males leaving during playback, five males approaching, and six males not responding at all ($L = 5$, $P = 0.58$). No females responded to playbacks.

Behavior during agonistic encounters between males.—Hummingbirds exhibited an array of postures and sounds associated with agonistic interactions. Some activities occurred in conjunction with others, e.g., sounds uttered when the bird was crouched with a spread tail. Such composite displays were quite common.

We observed wing waving, in which wings were elevated and vibrated, only eight times, but as it occurred very rapidly, many probably were not detected. Each case occurred when a resident was approached by another male, or another male flew directly over the perched resident. Usually the resident's tail was spread, and sometimes the bird emitted a Single Chip or *Zeet*. The opponent then left. Tail spreading occurred alone or in combination with many other acts and exposed the prominent white tail spots. In some cases the tail also vibrated rapidly.

Chases varied greatly in duration; some were very long, apparently covering more than the length of one territory. They often were initiated by one bird flying directly toward another, but as both birds disappeared

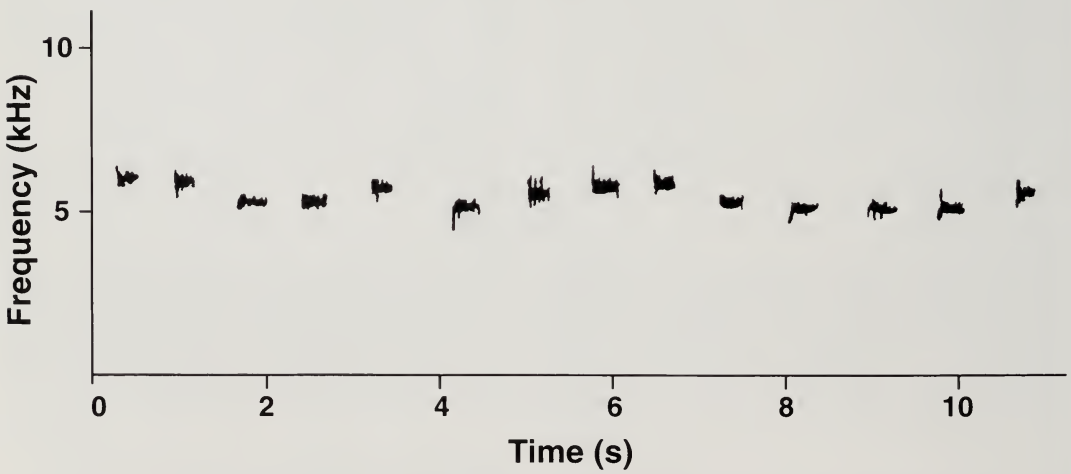

FIG. 2. Sonogram of male Blue-throated Hummingbird (*Lampornis clemenciae*) Serial Chips showing pitch shifts. Recorded by S. J. Taylor at Southwestern Research Station, southeastern Arizona, June, 1995. Prepared using Canary 1.2.

from view quickly, we could not distinguish between shorter supplantings and longer chases. Long chases involving three (and more rarely four birds) were frequent, particularly early in the breeding season, but were impossible to follow in detail. One bird chased another, with the third bird joining later. Males sometimes supplanted females, but long intersexual chases were uncommon except in a sexual context. Male Blue-throated Hummingbirds, the dominant species, sometimes chased male Magnificent Hummingbirds, but heterospecific encounters were rarer and briefer than conspecific ones. Encounters with Magnificent Hummingbird males were confined to chases and did not include hovers or crouches described below.

Another type of interaction involved crouching in which a perched bird (resident) was approached by another (intruder) that hovered within a few centimeters of the resident. The outcome was variable. A chase sometimes ensued immediately with the resident pursuing the intruder. Alternatively, the perched resident crouched with tail spread. The position of the hovering bird sometimes changed from a frontal approach to hovering directly over the resident, and in rare cases the intruder even landed on the back of the crouched bird. An even more unusual posture occurred in which the crouched bird fell over backwards and hung upside down while the opponent continued hovering over it (see drawings in Rising 1965). The bird that crouched always won ($n = 31$ encounters); the bird that approached the resident left or was chased, in contrast to Rising's (1965) conclusion that the crouched bird was the subordinate.

A published videotape of male Blue-throated Hummingbirds (Nature Science Network, Inc. 1988) allowed slow motion analysis. Initially the resident (R) was perched, the intruder (I) landed next to R, and then I flew and hovered over R. R shifted position and hung upside down with his tail spread and bill pointed upward at the hovering I, who had its bill pointed at R (at one point their bills almost touched). I changed position, and the two birds briefly were tail-to-tail (R was still upside down). I called and moved, still hovering a few centimeters above R. R righted itself on the perch but maintained tail spread as I hovered over it. I left and R remained. Hanging upside down was relatively rare in our sample of crouches (19.4%, $n = 31$), and we never observed one with a bill-to-bill component as in this video.

TABLE 3. Male and female Blue-throated Hummingbirds (*Lampornis clemenciae*) differed in the number of intrasexual agonistic acts and associated vocalizations. Data are from the Southwestern Research Station, southeastern Arizona, April through June, 1995–2000.

	Agonistic activity					
	Chase		Crouch		Hover	
Call type	Male-male	Female-female	Male-male	Female-female	Male-male	Female-female
Long call	13	0	0	0	0	0
Short call	4	0	9	0	3	0
Zeet	6	0	4	0	4	1
Bill crack	6	0	0	0	10	1
No calls	8	9	18	5	5	6
Total	37	9	31	5	22	8

Hovering was another type of confrontation (Table 3) in which both birds flew up face to face only a few centimeters apart with widely spread tails, sometimes flying several meters into the air while maintaining the same orientation. Hovers sometimes terminated in chases.

Agonistic sounds.—Various sounds were associated with agonistic interactions. One was a trill (unit B), a common component of male songs (Ficken et al. 2000), and the only song unit delivered without any accompanying units. The B unit occurred in several different contexts. The loud Staccato Trills (Fig. 1b) occurred during some agonistic encounters. Soft Trills of much lower amplitude with shorter internote intervals than the staccato ones sometimes occurred during close range agonistic interactions between males, and all apparent copulations were preceded by these whispered sounds. We excluded these trills from the quantitative analysis of sounds during encounters (Table 3) because the soft ones were inaudible unless we were within a few meters of the bird.

Bill Cracks were nonvocal sounds (Fig. 1c) produced during hovers and chases (Table 3). In the few cases where we had good views of the combatants, the sounds were produced as the birds hovered and struck bills at about 2/

3 the length of the bill. The sounds were loud, indicating a forceful impact. Bill Cracks occurred during chases when the bird being chased turned and confronted its pursuer. Bill Cracks were not heard during crouches.

Four major types of vocalizations also occurred only during agonistic interactions. The *Zeet* was a short, harsh, snarly call of variable duration, covering a wide frequency range (Fig. 1d). Short Calls were a series of several (typically 3) transients covering a wide frequency range (Fig. 1e). Long Calls (Fig. 1f) were more protracted strings of notes with more complex structure than Short Calls. We recorded an unusually complex call only twice (both times delivered by the same male) during our extensive recording (Fig. 1g). Its rarity in our sample may be due to its occurrence in an unusual situation when two males hovered close to each other during an agonistic encounter near a sexually active female. Many of the notes in these calls are transients covering a wide frequency range. The Complex Long Call was more complex than other Blue-throated Hummingbird vocalizations except for song, as there was a mixture of note types, and some notes covered a narrower frequency range than is typical for other agonistic sounds such as Short Calls and the typical Long Calls.

Some sounds were associated with certain types of interactions more than others (Table 3). Long Calls were performed only during chases, while Short Calls and *Zeets* occurred during all three types of encounters (hovers, chases, and crouches). *Zeets* also were given when another individual flew near the caller but no obvious interaction occurred. They may inhibit approaches, in contrast to the other sounds that occurred once an interaction was already underway. Crouches often were silent, while hovers, and particularly chases, often had accompanying sounds.

Female territorial behavior.—We noted aggression between neighboring females at the time that sexual activity was occurring (late nest building and perhaps egg laying). This was the time that females uttered Serial Chips near the nests ($n = 3$ females). While feeders may have modified spatial relationships, most interactions were not near feeders. Two females were observed for several hours each on six days, and their territories did not overlap. One female had fledglings and later was observed lining a nest adjacent to an area where another female was engaged in the same activity. Both females were involved in many agonistic interactions with each other. Both returned to their original sites following encounters. We never observed agonistic encounters between incubating females or those with nestlings, despite about 20 h of observation.

The types of agonistic encounters between females included the same general categories as those of males (Table 3), but female encounters were of lower intensity. During 22 encounters, sounds occurred only twice. Chases usually were shorter as well as less frequent than those of males.

Male-female interactions.—During a period of about two days, the male often remained near the female and in the area of the nest. We observed behavior that seemed sexual, but because most birds were unmarked and the stage of the nesting cycle for many females was unknown, we were able only to piece together a number of separate observations to produce a general pattern. Females sometimes approached singing males and produced a very distinctive but muted song that often overlapped the male's song (Ficken et al. 2000). In all cases where visibility was good, the female left after <10 s. On one occasion when there were no prior interactions, a male hovered over a crouched female. She uttered a *Zeet* and he left, but he returned about 5 min later to the same place and delivered long songs. The female then disappeared from view.

Male-male interactions near females.—The period of late nest building through nest completion coincided with sexual behavior and was marked by especially intense agonistic encounters between males, often involving long chases. This was the only time we observed physical contact between males. On three different occasions males tumbled to the ground, hitting with a strong impact ("thuds" were heard) with one grasping the other. Females always were nearby.

Female sexual invitation behavior.—An unusual aerial display that we named "River Dance" was performed only by females known to be sexually active, just following nest completion and during the period of *Tia* calling (see below). Just prior to dancing, a

female would be perched very low near a creek or would fly to the site of the dance. All dances took place over a creek, a dry creek bed, or more rarely (<10% of cases) <10 m from a creek. Dances did not take place near nests. Dances may have originated from ritualized insect-catching movements, but no insects were present as we inspected the sites carefully immediately after dances. No dances were observed during a study session in which no females were at the right stage of the nesting cycle.

River Dance was a series of short flights, usually only a few cm high and 1–3 m in diameter, often centered over the creek. The female did not vocalize during the dance, and she was quiet before starting a display. Each short flight was followed by a hover (typically <2 s long) and a change in position. During some but not all hovers, females exposed their white outer tail feathers, sometimes while flicking the tail back and forth. Dances incorporated all directions (up, down, left, right, forward, backward, and diagonals) in 3-dimensional space. Mean duration (timed from video recordings) was 12.4 s ± 6.0 (n = 19), with about 10 movements per dance. In some cases we observed males within a few meters of the dancer, but in many cases we were not certain if males were present, as they tended to perch low in very dense vegetation and chipped only occasionally. We observed no interactions immediately following the dances.

During periods of sexual activity, females uttered special calls (*Tias*) that were not heard at other times. We measured the calls from a pooled sample of females (≥3 different birds, 8 sonograms); mean duration was 0.58 s ± 0.25, highest frequency was 7.89 kHz ± 0.76, and lowest frequency was 5.75 ± 0.09. Unlike Serial Chips, *Tia* calls consisted of a series of rapid chip notes with the first note always longer and slightly higher pitched than the others (Fig. 1h).

The calls were given either when the bird was perched or when she flew. In contrast to many calls of this species, *Tias* were unusually loud, and functioned as long distance signals, as individuals ≥50 m distant approached in response to the calls. Because of observational difficulties, the stimuli eliciting the calls were not always apparent. Sometimes females seemed to call spontaneously, but at other times they called in response to a male flying overhead. Some calls from perches elicited no apparent responses from other birds. On other occasions the female called in flight as she approached and then engaged in a chase with a male, although it was not clear which sex was the ultimate pursuer. In one case, a female uttered a very muted *Tia* as the male hovered over her, but no further interactions took place. In two instances encounters with *Tias* ended in copulations.

We also conducted seven playbacks of *Tias*. Responses occurred at all sites where we had observed females calling that day. In all cases the females approached, and in three cases she uttered *Tias,* chipping only once. In four of the seven cases a male also approached during playback. One time the male chased the female, and another time two males approached and chases ensued. In two other cases, chases occurred but the sexes of the participants could not be determined.

Copulations.—We observed three probable copulations, and E. Sandlin (pers. comm.) provided data on another. All happened during late May or early June at the Southwestern Research Station. The events occurred very rapidly and cloacal contact was not observed. All were on the ground in dense vegetation at low light levels during early morning or evening. In three cases a chase preceded copulation, in two cases *Tias* occurred, and in all four cases the male performed a soft B trill fragment.

Calls of the young.—Nestlings were silent, as was the female in approaching the nest, giving only a soft call when a human was near the nest (Wagner 1952; MSF unpubl. data). However, fledglings called prior to a feeding when the female was several meters away, and sometimes in her absence. Sometimes the female also chipped before approaching the fledglings for feedings (Wagner 1952; MSF unpubl. data). When the female was close, the young quivered their wings. The chips uttered by fledged young just before independence differed from the other chips in the species' repertoire (Table 2) in being higher pitched, with the main band between 7.9–9.4 kHz and a second band around 20 kHz.

Calls in response to a predator.—We observed only one case of a reaction to a pred-

ator, a Northern Pygmy-Owl (*Glaucidium gnoma*), which was perched about 1 m from a feeder. Five Blue-throated Hummingbirds (unknown sex) flew at the owl giving loud chips. The owl then flew and was followed closely by the chipping hummingbirds. Calls of different individuals overlapped, a pattern often associated with oscine mobbing (MSF unpubl. data). Because of these conditions, the exact number of individuals calling was unknown. Mobbing Chips (Table 2) were of shorter duration than either male or female chips ($t = 11.3$, df = 37, $P < 0.0001$) and were higher in frequency ($t = 3.38$, df = 23, $P = 0.030$) compared to female Single Chips. Mobbing Chips also differed from other types of chips in having a second band ranging from 7.8–9.3 kHz ($n = 10$; Fig. 1i), instead of the usual harmonic band for Single Chips or Serial Chips.

Another type of call, described as a "squeal," is uttered by both sexes and young in stressful situations, such as being handled (Williamson 2000).

DISCUSSION

Reproductive behavior.—As hummingbirds are polygynous with no pair bonds and no male parental care, females would be expected to exert strong selection for male traits. In many hummingbirds extreme sexual dimorphism, brilliant male colors, and often acrobatic aerial displays are associated with courtship (Wagner 1954, Johnsgard 1997, Schuchmann 1999). In Blue-throated Hummingbirds, sexual dichromatism is minimal, the male being distinguished from the female by a blue gorget, and in the dim light of its typical habitat even that difference may not be readily apparent. No aerial displays or exaggerated visual signals by males are associated with courtship (Wagner 1954; MSF unpubl. data).

Our observations of the reproductive behavior of Blue-throated Hummingbirds revealed some new aspects of hummingbird behavior. Unusual features included female territoriality near the nest, active and complex role of females in initiating sexual encounters (including aerial displays), courtship occurring in several stages, and the diversity and complexity of communicatory signals.

Males of many hummingbird species are territorial, and Blue-throated males are noted for being very aggressive. However, time budgets showed that the use of more energetically expensive behavior involving flights (short chases, hovering, and the long chases characteristics of this species) were rarer than the presumably lower cost vocalizations. The discovery that vocalizations are an important component of hummingbird territory maintenance is not new, having been suggested previously for the highly vocal Anna's Hummingbird (Stiles 1982, Powers 1987).

These hummingbirds were unusual in having two different vocal systems involved in territorial behavior. Oscine song typically serves dual roles in territorial advertisement and mate attraction (Catchpole and Slater 1995). Blue-throated Hummingbirds have partitioned these functions in a different way, with song mediating close range interactions between males and attracting females. Serial Chips, on the other hand, were involved only in long distance territorial advertisement.

Males advertised territorial boundaries through strings of loud Serial Chips often from an exposed perch near a stream, whereas songs were low amplitude and sometimes were delivered when a male was hidden. Blue-throated Hummingbirds preferred riparian habitat, a noisy environment in which chips probably were effective for long distance communication. Head turning movements during chipping broadcast the signal in many directions and increased its effectiveness. Even when silent, they were alert and surveyed their environment, immediately pursuing conspecific interlopers. Chipping birds usually were not approached by conspecifics.

Playback results also strengthened our interpretations that Serial Chips and song had different roles in territorial behavior, as close approach to playback was associated only with song. Serial Chips seemed to transmit the message of territory occupancy, and may inhibit intrusions by other males. Song also indicated ownership, but was not the primary means of excluding other males, serving instead as a short distance threat (characterized by very low amplitude). Song often was associated with agonistic encounters, and other males sometimes approached a singer. Other indications for song playing a strong role in sexual behavior were that longer songs (hence more complex ones), and longer singing bouts

occurred when reproductive activity was at its height. In oscines, female preference for song complexity is an important component of sexual selection for many species (Catchpole and Slater 1995). In Blue-throated Hummingbirds where the male and female may not share feeding areas (Wagner 1952), sexual contact is limited, and the male does not participate in parental care, female choice may be based at least in part on characteristics such as song composition, song length, and bout composition.

Males did not respond to playback of female song. Under natural conditions female singing usually occurred only when she was close to the male (Ficken et al. 2000), so it is not surprising that males did not respond to playback of this song in her absence.

Females defended an area near the nest against other females from late nest building until completion of egg laying (Wagner 1952; MSF unpubl. data). Serial Chips by females evidently serve as territorial advertisement during the few days of sexual activity. The most likely hypothesis for this short term defense of a site where sexual activity occurred is that females competed for access to males. As nests had already been constructed, females' competition for access to nest locations is an unlikely explanation for female aggressive behavior.

Montgomerie and Thornhill (1989) noted that loud calls of female Red Junglefowl (*Gallus gallus*) and Lapland Longspurs (*Calcarius lapponicus*) during the fertile periods attracted males, and suggested that the phenomenon is more widespread, and that the calls advertise fertility and incite male-male competition. They predicted that such calls should be most common in species that are not strictly monogamous. They noted the difficulty of studying such calls in the wild because fertile periods of birds are so short. We heard calls only when females were in the preincubation period. The calls were exceptionally loud for hummingbirds, and experiments supplemented our observations that males approached calling females and if more than one male was present intense male-male competition resulted (MSF unpubl. data). As the sexes often were spatially segregated, vegetation was dense, and females were sexually receptive only a few days for each brood, the importance of female signaling sexual readiness was apparent. Females may be unreceptive to male approaches, even reacting with snarling attacks (Williamson 2001; MSF unpubl. data).

The traditional view of hummingbird courtship is of advertising males and relatively passive females (Johnsgard 1997, Schuchmann 1999). In contrast, female Blue-throated Hummingbirds were very active in initiating sexual activities. Females may evaluate a male's fitness based on his singing, by his response to her behavior, such as *Tias* and River Dance, and by his pursuit chases. Furthermore, as male-male competition also was intense during this period, females may selectively mate with the winners of those contests, as those males were more likely to remain nearby. Males on the other hand, had the opportunity to assess female fitness based on her precopulatory activities.

While there were no reports of copulations for this species in the literature (there are very few for any hummingbird species), these events shared some similarities with a report of copulation in the Magnificent Hummingbird (Stiles pers. comm. *in* Powers 1996), another species lacking male aerial courtship displays. The sexual behavior followed singing by the male who then chased the female to a low perch and uttered whisper songs while facing her. Cloacal contact followed alighting on her back, with only a few seconds of contact.

Communicatory repertoire.—We have described the major communicatory signals of this species, allowing us to assess repertoire size, diversity, and usage, and make preliminary comparisons with some other species. Indications that hummingbirds are a neglected group is provided by the most recent bibliography of avian vocalizations that lists 359 publications, with only one on hummingbirds (Hansen 1997).

Decisions on classifying and determining the size of vocal repertoires often are difficult because of intermediates (grading) and other problems arising from the lack of distinct categories (Hailman and Ficken 1996). On the basis of acoustic properties and usage, we identified 16 acoustic signals in Blue-throated Hummingbirds (male song, female song, female *Tia,* male Soft Trill, Staccato Trill, *Zeet,* Long Call, Complex Long Call, Short Call,

female Single Chip, male Single Chip, male Serial Chip, female Serial Chip, Fledgling Chip, Mobbing Chip, and distress Squeal). Bill cracks occur during agonistic encounters as an outcome of physical contact, but may have communicatory salience. In addition, wing buzzes could have signal functions.

Many of the sounds produced by these hummingbirds were acoustically simple. The most complex vocalization, male song, consisted of an array of different notes with a precise syntax (Ficken et al. 2000). Female song consisted of a more limited number of different notes and was of shorter duration (Ficken et al. 2000). The Long Call occurring in agonistic encounters usually was a repetition of a single note, but more rarely an array of diverse notes (Complex Long Call).

Some diversity of messages may be achieved by slight modifications of acoustic structure. For example, the B unit, a common element in male songs (Ficken et al. 2000), served as a precopulatory call when at low amplitude and not accompanied by other song elements. On the other hand, a loud version with longer internote intervals and a staccato quality (Staccato Trill) was associated with aggression and never with sexual encounters (Ficken et al. 2000). These hummingbirds utilized chips, some with slight but consistent differences in several contexts, and some differences probably were indicative of different messages. For example, Fledgling Chips were higher pitched than other chips, as might be expected of a short range signal. Single Chips may serve as an announcement of presence, and here the sexes differed. Females not only chipped much less frequently than males, but their chips also were much shorter, although about the same pitch as those of males. Serial Chips by both sexes were delivered in different circumstances than Single Chips, and evidently served as territorial advertisement. The female sexual call (*Tia*) was a string of very rapid short chips of a different quality than other sounds in the repertoire. Mobbing Chips exhibited some frequency and temporal differences when compared with other chips.

Interspecific comparisons of vocal repertoires are even more difficult than intraspecific ones, but some insights may arise from generalities among communicatory categorization in unrelated species. In petrels, a well-studied group of nonpasserines, functional categories of vocalizations include food begging of young, copulation calls, agonistic calls, contact calls (to avoid others during flight), and those used in courtship and agonistic behavior for a total of 6–8 different calls (Bretagnolle 1996). Blue-throated Hummingbird vocalizations fell into similar general functional categories, but this species lacked contact calls and had more elaborate sexual and agonistic signals than petrels, as well as two calls used for predators (mobbing and distress). A nonoscine passerine, the Eastern Phoebe (*Sayornis phoebe*), has nine vocalizations (Smith 1977). The Black-capped Chickadee (*Poecile atricapilla*) has a repertoire of about 13 different vocalizations (Hailman and Ficken 1996). A pinnacle of repertoire size is the 26 sound signals of the Village Weaver, *Ploceus cucullatus* (Collias 2000). With about 16 different vocalizations, Blue-throated Hummingbirds were at the high end of the number of different acoustic signals in an avian species' repertoire, although the complexity of the sounds (except for male song), was not as great as that of most oscines. It is impossible to do more than approximate the actual number of signals based on structure and usage without performing experiments to determine how Blue-throated Hummingbirds categorize calls.

The variety of visual signals was more limited than the vocal repertoire and involved tail, wing, and body movements. Tail spreading and rapid tail shuffling occurred in several contexts and exposed the large white tail spots of both sexes. Wing waving served as a threat when another hummingbird approached. Crouching was more graded, varying from a slight crouch to the bird actually falling over backwards on the perch. Not only was this a complex series of postures, but the message potential also was extended by a variety of sounds associated with these acts. Such multimodal signals can provide more information than signals using only one sensory modality (Partan and Marler 1999).

Some differences between hummingbird species with aerial displays and Blue-throated Hummingbirds may be related to ecological conditions. Those with aerial displays often inhabit more open areas than Blue-throated Hummingbirds. Blue-throated Hummingbirds

favor shaded riparian areas, and their plumage dichromatism is limited. The evolution of complex song probably was related to difficulties in detection of visual signals in these dense habitats (Ficken et al. 2000).

Complex signals by females may be related to being multibrooded with little territorial overlap with males. In the absence of female signals, such as *Tias* and River Dance, the male would have little opportunity to assess female reproductive state. In addition, the complex interactions of the sexes allowed both the male and female to assess fitness attributes of the other, and thus affect mate choice. Until recently, most studies of bird behavior, particularly those of vocalizations, have focused on songbirds. Clearly, other groups, such as hummingbirds, warrant more attention.

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HABITAT CHARACTERISTICS IN THE CORE BREEDING RANGE OF THE SWAINSON'S WARBLER

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ABSTRACT.—I investigated the physiognomic and floristic characteristics of Swainson's Warbler (*Limnothlypis swainsonii*) territories at five localities within its core breeding range in Arkansas, Mississippi, Louisiana, and Florida. The warbler attained its greatest abundance (10–20 territorial males/km^2) in floodplain forest characterized by small (<25 cm dbh) trees (ca 620–820 stems/ha) and understory thickets of saplings, vines, and shrubs (ca 35,000–48,000 small woody stems/ha). Territories in mature forest typically were associated with disturbance gaps. Canopy height, basal area, and floristics appear to be relatively unimportant factors in habitat selection, provided that understory requirements are met, which explains the warbler's occurrence in regenerating clearcuts as well as in relic tracts of old growth forest. Giant cane (*Arundinaria gigantea*), hypothesized to be an essential habitat requisite along the northern periphery of its breeding range, was sparse or absent in the prime breeding locations surveyed in this study. Selective thinning and clearcutting are viable habitat management techniques for the Swainson's Warbler. *Received 28 August 2001, accepted 28 February 2002.*

The success of management programs for Nearctic-Neotropic migratory birds ultimately will depend upon a thorough understanding of the fundamental habitat requirements of breeding and wintering populations. This understanding typically is acquired in incremental phases, beginning with the compilation of life history anecdotes and narrative descriptions of habitat (Brewster 1885, Wayne 1886, Widmann 1895) and the mapping of breeding and wintering distributions (Robbins et al. 1992, Remsen 2001). Once general habitat preferences are known, research customarily shifts toward the quantification of habitat structure (Eddleman et al. 1980), investigation of nesting and foraging microhabitats (Robinson and Holmes 1984, Parrish 1995, Graves 1998), surveys of geographic variation in habitat structure (Dow 1968; Collins 1983a, 1983b; James et al. 1984), and the correlation between measurable features of the environment and distribution and abundance of populations (Orians and Wittenberger 1991, Stowe et al. 1993). In the final phase, researchers examine the influence of spatial and compositional attributes of habitat on the fecundity and viability of populations (James et al. 1997). Although considerable progress in habitat analysis has been made during the past 50 years (Wiens 1989), investigative studies on the majority of migratory species are still firmly mired in the secondary phase of diagnosis and quantification (see accounts in Poole et al. 1992–1993; Poole and Gill 1993–1997; 1998–2002).

This paper addresses the physiognomic and floristic characteristics of habitat in the core breeding range of the Swainson's Warbler (*Limnothlypis swainsonii*). Though locally common in the lower Mississippi Valley and on the coastal plain from eastern Texas to southeastern Virginia (Meanley 1971, Brown and Dickson 1994, Graves 1998, Winker et al. 2000), this warbler currently is ranked as the second most endangered breeding songbird in the southeastern United States because of habitat destruction on its breeding range, relatively low population density, and a small wintering range in the Caribbean basin (Morse 1989; Terborgh 1989; Hunter et al. 1993, 1994; Smith et al. 1993; Thompson et al. 1993; Brown and Dickson 1994; Rappole 1995; Mueller et al. 2000). Despite the attention and financial resources focused on the Swainson's Warbler by conservation organizations over the past two decades, surprisingly little is known about its fundamental breeding habitat requirements (Graves 2001). Narrative descriptions of habitat are plentiful, but these offer only a fragmentary characterization of the factors relevant to the warbler's breeding biology (e.g., Brewster 1885; Wayne 1886; Beckham 1887; Widmann 1895; Brooks and Legg 1942; Meanley 1945, 1966, 1969, 1971; Sims and DeGarmo 1948; Brown and Dickson

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1994; Graves, 1992, 1998; Carrie 1996; Graves et al. 1996). As a direct consequence of the warbler's secretive behavior and large territory size (3–18 ha), and the difficulty of conducting field work in the inhospitable, frequently impenetrable, floodplain habitat favored by this species, the critical mass of quantitative data required for the design and implementation of sound conservation policy is lacking.

Quantitative studies of the physiognomy and floristics of Swainson's Warbler habitat have been conducted in its core breeding range in South Carolina (Peters 1999) and Louisiana (Bassett 2001), and near the northern margin of the breeding range in Illinois (Eddleman 1978, Eddleman et al. 1980), Missouri (Thomas et al. 1996), and the Great Dismal Swamp, Virginia (Graves 2001). Conclusions drawn from these studies, however, are somewhat contradictory. Most notably, Eddleman et al. (1980) and Thomas et al. (1996) stressed the importance of giant cane (*Arundinaria gigantea*) as a critical component in habitat restoration plans for declining populations of Swainson's Warblers in Illinois and Missouri. However, substantial populations of Swainson's Warblers are known to occur in many localities within the core breeding range where cane is either scarce or absent (Graves 2001). Such geographic variation in habitat use is a well-known behavioral phenomenon among passerine birds and correlations between habitat occupancy and specific components of breeding habitat frequently exhibit significant regional fluctuations (Dow 1968; Collins 1983a, 1983b; James et al. 1984). Collectively, these studies suggest that habitat management and conservation efforts in the core breeding range of the Swainson's Warbler should not be predicated on data obtained from geographically peripheral populations.

This study was not designed to evaluate habitat selection of the Swainson's Warbler—the comparison of occupied sites to those available within a local area. Rather, my objective was to evaluate geographic variation in the physiognomic and floristic characteristics of territories in order to address three principal questions: (1) Does the physiognomy of territories vary geographically? (2) Is giant cane an essential element of breeding habitat? (3) Are there regional differences in the litter-producing tree species found on territories? Finally, I discuss the pertinence of physiognomic and floristic data to habitat management programs.

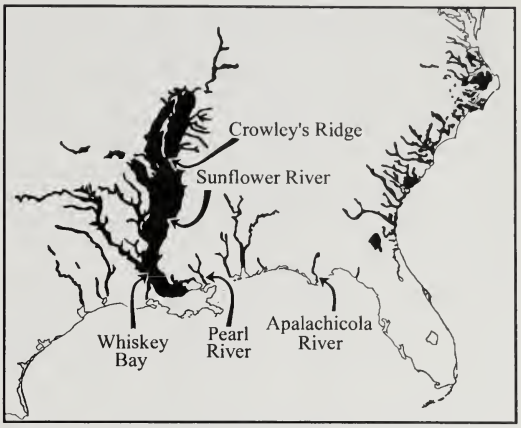

FIG. 1. Study sites depicted in the potential distribution (black) of floodplain deciduous forest and pocosins in the southeastern United States (redrawn from Kuchler 1966), which support the bulk of contemporary breeding populations of Swainson's Warbler.

METHODS

Habitat assessment.—I censused breeding populations of Swainson's Warblers along transects in large (>8,000 ha) tracts of floodplain forest on public lands (Fig. 1) with the aid of "playback-and-follow" trials (Graves 1996). The location of territories was recorded on soil survey maps prepared by the USDA Soil Conservation Service. I randomly chose territories for habitat analysis. Employing the sampling methods outlined by Graves (2001), I centered a circular sampling plot (0.045 ha, diameter = 24 m) at the first terrestrial site in each territory at which the undisturbed male was observed to both sing and forage (n = 49 territories). The Swainson's Warbler is a terrestrial dead leaf specialist that feeds primarily on litter arthropods whose availability is linked to the characteristics of soil and leaf litter (Graves 1998, 2001). A substantial body of data indicates that males and females use similar foraging microhabitats (Graves 1998). Sampling at dual purpose singing-foraging sites ensured that the physiognomic and floristic data obtained actually corresponded to microhabitats used by Swainson's Warblers. I located sampling plots 40–200 m from roadsides to minimize edge effects, although Swainson's Warblers may actually prefer roadside habitat in certain instances (Graves 2001). Four additional plots in the Whiskey Bay study area (see site descriptions, below) were centered at active nests near singing stations. Data from these nesting sites were collected after the nests were destroyed by predators or the young had fledged.

I measured 14 habitat characteristics in each plot (one plot per territory). Trees (>5 cm dbh) occurring in 0.045-ha plots were measured to the nearest cm and identified to species. I calculated basal area from raw field measurements, whereas stem diameter was converted to size class for comparison. I identified and counted all woody vines supported by trees (at 1.4 m above ground). I also identified and counted small woody stems (<5 cm dbh; i.e., shrubs, tree saplings, woody vines, cane) in four circular subplots (12.6 m^2, diameter = 4 m) positioned at the cardinal compass coordinates on the perimeter of the 0.045-ha plot. I obtained exact counts by clipping all small stems within each circular subplot at a height of 0.5 m above ground.

Flooding has a profound influence on habitat occupancy patterns of the Swainson's Warbler (Meanley 1966, 1971; Graves 2001). I did not incorporate hydrological data (presence of standing or pooled water) in the analyses, however, because of variation in the interval (1–78 days) between the marking of foraging sites and the subsequent collection of vegetation data.

Site descriptions.—I conducted the study at five sites (Fig. 1). (1) Crowley's Ridge (34° 38′ N, 90° 39′ W), St. Francis National Forest, Lee and Phillips counties, Arkansas. This study area paralleled the ecotone between Crowley's Ridge, a loess formation of Pleistocene age, and the floodplain of the St. Francis and Mississippi rivers. Second growth forest along the census transect included typical floodplain taxa (e.g., *Carya aquatica*) as well as those species restricted within the Mississippi Embayment to Crowley's Ridge (e.g., *Lireodendron tulipifera*). Soils were Convent silt loams (coarse-silty, mixed, nonacid, thermic Aeric Fluvaquents; Hogan and Gray 1974, Gray 1977). Males establish breeding territories on the Gulf Coastal plain and in the lower Mississippi Valley during the second and third weeks of April (Meanley 1971, Brown and Dickson 1994). I marked foraging sites 4–7 May 1993 (n = 6) and collected habitat data 5–7 May 1993. Population density in the study area was ca 3.8 males/km^2.

(2) Sunflower River (32° 51′ N, 90° 46′ W), Delta National Forest, Sharkey County, Mississippi. I sampled territories on the floodplain of the Big Sunflower River in second growth forest (n = 7) and in the largest remaining tract of old growth forest (n = 3) in the Mississippi Delta, all on Sharkey clay soils (very-fine, montmorillonitic, nonacid, thermic Vertic Haplaquepts; Scott and Carter 1962). I marked foraging sites from 25 April to 1 May 1993 and collected habitat data from 28 April to 2 May 1993. Population density in the study area was ca 4.8–9.3 males/km^2.

(3) Whiskey Bay Pilot Channel (30° 24′ N, 91° 40′ W), Sherburne Wildlife Management Area and Atchafalaya National Wildlife Refuge, St. Martin Parish, Louisiana. The study site on the east bank of the main channel of the Atchafalaya River was dominated by second growth deciduous forest (10–50 years old) on Convent silt loam soils (Murphy et al. 1977). The eye of Hurricane Andrew passed directly over the study area on 26 August 1992, causing moderate canopy damage and scattered windthrow (Doyle et al. 1995). I marked foraging and nesting sites from 26 April to 10 May 1994 (n = 14 foraging sites; n = 3 nests) and 10 May 1995 (n = 1 nest); B. L. Tedford collected habitat data from 27 April to 30 June 1994 and on 10 June 1995. Population density in the study area was ca 11.3–14.2 males/km^2.

(4) Pearl River (30° 25′ N, 89° 43′ W), Bogue Chitto National Wildlife Refuge and Pearl River Wildlife Management Area, St. Tammany Parish, Louisiana. The study site on the floodplain of the Pearl River was characterized by second growth forest of mixed age (10–60 years old) on Arktabutla and Rosebloom soils (fine-silty, mixed, acid, thermic Aeric Fluvaquents; Trahan et al. 1990). I marked foraging sites from 25 April to 6 May 1995 (n = 7 territories); B. L. Tedford collected habitat data 1–23 July 1995. Population density in the study area was ca 20.5 males/km^2.

(5) Apalachicola River (30° 04′ N, 89° 43′ W), Liberty County, Florida. The study site on the floodplain of the Apalachicola River in the Apalachicola National Forest was a patchwork of regenerating clearcuts (mostly 1–8 m high) and tracts of taller second growth deciduous and mixed deciduous-pine forest (20–30 m) on Meggett loam soils (fine, mixed, thermic Typic Albaqualfs; USDA Soil Conservation Service unpubl. data). I marked foraging sites 28–30 April 1996 (n = 12 territories); B. L. Tedford collected habitat data 9–13 June 1996. Population density in the study area was ca 5.6 males/km^2.

Statistics and hypothesis testing.—I tested variables for goodness of fit to a normal distribution with Lilliefors test. Nine of 14 variables exhibited significant deviations from normality even after being subjected to variance-stabilizing transformations. Therefore, I used a series of nonparametric one-way analysis of variance tests (Kruskal-Wallis ANOVA) to evaluate geographic variation among physiognomic and floristic variables (Table 1). Significance values were Bonferroni adjusted for the number of simultaneous tests (P = 0.05/14). The univariate relationship between selected pairs of variables was evaluated with Spearman rank correlation coefficients. Covariation among variables was evaluated with principal components analysis (PCA) of correlation matrices for transformed variables. This procedure transforms a group of generally correlated variables into a set of uncorrelated composite variables and is particularly useful for reducing the dimensionality of complex data sets for graphic presentation. All analyses were performed with SYSTAT ver. 9 (SPSS, Inc. 1998).

RESULTS

Kruskal-Wallis ANOVA revealed significant geographic variation in 8 of the 14 habitat variables, although locality medians were relatively similar in magnitude for most variables (Table 1). For example, although the basal area of trees (BAS) on individual plots had a range of 6.1–87.4 m^2/ha, locality me-

TABLE 1. Ranges (medians) of physiognomic and floristic variables measured on 0.045-ha plots in 53 territories of the Swainson's Warbler at five localities in the core breeding range of the species in the southeastern United States, 1993–1996.

Code	Variable	Localities					Kruskal-Wallis ANOVA	
		Crowley's Ridge (n = 6)	Sunflower River (n = 10)	Whiskey Bay (n = 18)	Pearl River (n = 7)	Appalachicola River (n = 12)	χ^2	P^a
BAS	Total basal area of trees (dbh > 5 cm) m²/ha	21.7–52.8 (26.0)	14.6–87.4 (29.3)	9.3–33.1 (16.8)	7.8–16.0 (13.0)	6.1–42.9 (13.7)	19.60 (18.2)[b]	0.0006
ONE	Trees (dbh = 5–14.9 cm)/ha	333–1,244 (467)	111–422 (233)	422–1,956 (711)	378–644 (489)	178–1,111 (644)	21.32 (511)	0.0003
TWO	Trees (dbh = 15–24.9 cm)/ha	44–133 (122)	22–222 (67)	22–356 (111)	111–378 (133)	44–289 (100)	6.69 (111)	0.15
THRE	Trees (dbh = 25–39.9 cm)/ha	0–133 (67)	0–133 (56)	0–133 (89)	0–89 (44)	0–244 (44)	4.62 (44)	0.33
FOUR	Trees (dbh = 40–59.9 cm)/ha	0–89 (33)	0–67 (33)	0–89 (0)	0–44 (0)	0–156 (11)	7.85 (22)	0.097
FIVE	Trees (dbh = 60–79.9 cm)/ha	0–89 (22)	0–22 (0)	0–22 (0)	0 (0)	0–22 (0)	22.96 (0)	0.0001
SIX	Trees (dbh > 80 cm)/ha	0 (0)	0–44 (0)	0–22 (0)	0 (0)	0 (0)	13.86 (0)	0.008
TREE	Trees (dbh > 5 cm)/ha	600–1,422 (789)	267–822 (433)	667–2,156 (1,044)	555–1,022 (689)	289–1,267 (878)	20.50 (778)	0.0004
TSPE	Tree species (dbh > 5 cm)/0.045 ha	7–15 (11.5)	4–10 (5.5)	5–13 (8)	6–10 (8)	3–9 (7)	16.93 (8)	0.002
VINE	Vines (including *Smilax*) supported by trees/ha	2,773–15,067 (5,111)	2,044–7,089 (4,578)	755–5,955 (2,444)	1,600–5,755 (3,111)	222–3,267 (1,022)	25.87 (2,744)	<0.0001
VSPE	Vine species/0.045 ha	8–11 (9.5)	7–9 (9)	3–9 (6)	8–12 (9)	2–8 (5)	34.92 (8)	<0.0001
CANE	Cane culms/ha	0–1,987 (0)	0–73,118 (0)	0 (0)	0 (0)	0 (0)	10.64 (0)	0.03
SHRU	Woody stems (dbh < 5 cm)/ha	17,087–79,476 (44,903)	8,742–63,183 (28,313)	7,550–104,710 (34,969)	32,983–58,018 (48,281)	20,465–59,607 (32,585)	5.45 (34,773)	0.24
SSPE	Shrub species/50.3 m² (including tree saplings)	13–29 (17.5)	8–19 (15.5)	7–22 (14)	17–22 (20)	14–23 (17)	17.22 (16)	0.002

[a] Bonferroni adjustment: 0.05/14 = 0.0036; 0.01/14 = 0.0004; 0.001/14 = 0.00007.
[b] Median of data pooled across study sites.

TABLE 2. Tree species that composed more than 5% of the stems (dbh > 5 cm) in 53 territories of the Swainson's Warbler at five localities in the core breeding range of the species in the southeastern United States, 1993–1996. Total number of tree species at each locality is given in parentheses; values are percentages.

Tree species	Locality				
	Crowley's Ridge (28)	Sunflower River (17)	Whiskey Bay (23)	Pearl River (22)	Apalachicola River (18)
Liquidambar styraciflua (sweet gum)	12.2	14.8	—	25.1	18.1
Ulmus americana (American elm)	13.5	13.9	6.4	—	—
Acer rubrum (red maple)	—	7.2	7.4	—	5.2
Quercus nigra (water oak)	—	—	—	22.4	12.0
Acer negundo (box elder)	—	11.5	20.6	—	—
Celtis laevigata (sugarberry)	—	28.7	—	—	—
Cornus drummondii (rough-leaved dogwood)	—	—	26.0	—	—
Carpinus caroliniana (American hornbeam)	—	—	—	23.3	—
Pinus elliotii (slash pine)	—	—	—	—	20.0
Liriodendron tulipifera (tulip poplar)	13.5	—	—	—	—
Myrica cerifera (wax myrtle)	—	—	—	—	11.1
Forestiera acuminata (swamp privet)	—	8.6	—	—	—
Fraxinus pennsylvanica (green ash)	—	—	8.1	—	—
Sassafras albidum (sassafras)	7.0	—	—	—	—
Platanus occidentalis (sycamore)	—	—	7.0	—	—
Cyrilla racemiflora (titi)	—	—	—	—	6.8
Halesia diptera (two-winged silverbell)	—	—	—	6.7	—
Quercus laurifolia (laurel oak)	—	—	—	—	6.6
Nyssa sylvatica (black gum)	—	—	—	—	6.6

dians varied from 13.0 m^2/ha (Pearl River) to 29.3 m^2/ha (Sunflower River). Substantial variability in basal area indicated that canopy height was a relatively unimportant factor influencing habitat use. Vegetation plots at all study sites were dominated by trees in the smallest size class (dbh = 5.0–14.9 cm; ONE), with locality medians varying from 233 trees/ha (Sunflower River) to 711 trees/ha (Whiskey Bay). The number of small trees (ONE) was highly correlated with the total number of trees (TREE) on vegetation plots ($r_s = 0.96$, $P < 0.0001$). There was no significant difference among sites in the frequencies of medium-sized trees (TWO, THRE, FOUR).

Scattered understory thickets composed of tree saplings, shrubs, and vines were the most conspicuous characteristic of breeding territories across the five study sites. The density of small woody stems (SHRU) on vegetation plots varied from 7,550–104,710 stems/ha. Locality medians for understory stems (SHRU + CANE) fell within a relatively narrow range of possible values: Sunflower River (31,592 stems/ha); Apalachicola River (32,585 stems/ha); Whiskey Bay (34,969 stems/ha); Crowley's Ridge (44,903 stems/ha); and Pearl River (48,281 stems/ha). The number of small trees (ONE) and small woody stems (SHRU) was uncorrelated ($r_s = -0.03$, $P = 0.83$).

High vine densities frequently were associated with canopy gaps and successional habitats favored by Swainson's Warblers. Regional variation in median vine density ranged from 1,022 vines/ha (Apalachicola River) to 5,111 vines/ha (Crowley's Ridge). The number of vines (VINE) and small woody stems in the understory (SHRU) was not significantly correlated ($r_s = 0.23$, $P = 0.091$). Giant cane (CANE) was uncommon at Crowley's Ridge (1 of 6 plots) and the Sunflower River (2 of 10 plots), and not observed at Whiskey Bay. Although scattered patches of cane occurred on the floodplains of the Pearl and Apalachicola rivers, none was recorded in vegetation plots in those areas.

The number of tree species (TSPE) per site ranged from 17 (Sunflower River) to 28 (Crowley's Ridge; Table 2). The high floristic diversity at Crowley's Ridge reflected a mixture of taxa restricted in eastern Arkansas to loess hills (e.g., *Liriodendron tulipifera*) with those species typical of floodplain habitats (e.g., *Carya aquatica*, *Liquidambar styraci-*

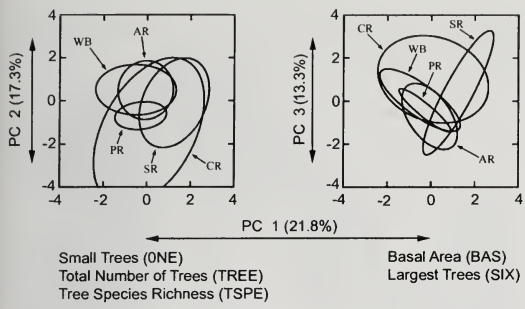

FIG. 2. Bivariate plots of 80% confidence ellipses surrounding factor scores produced by a principal components analysis of physiognomic and floristic variables of Swainson's Warbler habitat. Arrow indicates the direction of component loadings for variables that strongly influence the first principal component (PC 1). Locality codes: Apalachicola River (AR), Crowley's Ridge (CR), Pearl River (PR), Sunflower River (SR), and Whiskey Bay (WB).

TABLE 3. Principal component analysis of the correlation matrix among 14 physiognomic and floristic variables in 53 plots in territories of Swainson's Warbler in its core breeding range in the lower Mississippi Valley and along the Gulf coastal plain, 1993–1996. Correlation loadings >0.50 or <−0.50 are in boldface. Variable codes are presented in Table 1.

Variables	PC 1	PC 2	PC 3
BAS	**0.68**	0.03	**0.59**
ONE	**−0.81**	0.23	0.36
TWO	−0.44	0.17	0.23
THRE	0.36	0.40	−0.18
FOUR	0.38	0.12	0.03
FIVE	0.30	−0.42	0.33
SIX	**0.58**	0.04	**0.51**
TREE	**−0.78**	0.31	0.41
TSPE	**−0.52**	−0.42	0.49
VINE	−0.03	**−0.72**	0.33
VSPE	0.20	**−0.53**	0.28
CANE	0.30	0.31	0.31
SHRU	−0.13	**−0.56**	−0.38
SSPE	−0.14	**−0.71**	−0.29

flua). Cumulative species richness at each site was uncorrelated with the number of territories sampled ($r_s = -0.34$, $P = 0.34$). However, species richness within plots was positively correlated with the number of trees sampled ($r_s = 0.34$, $P = 0.013$). Each locality was dominated by a different species of tree, but no species composed more than 5% of the stems (>5 cm dbh) at each of the five study sites. The forest canopy at all localities was composed primarily of broad-leaved trees, although slash pine (*Pinus elliotii*) was frequent at the Apalachicola River site. The scarcity of hydrophytic species, such as bald cypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*), indicated that foraging and nesting sites were not subjected to prolonged flooding during the growing season (Table 2). Intra- and interlocality variation in the flora of territories offered additional confirmation that the warbler's breeding biology in floodplain habitats was not tied to the presence of a particular plant species (Graves 2001).

A principal components analysis of 14 habitat variables yielded three components (eigenvalues >1.5), which accounted for about half (52.4%) the variation recorded on plots in Swainson's Warbler territories (Fig. 2, Table 3). Principal component 1 (21.8% of the variance) discriminated vegetation plots with large trees (SIX) and high basal areas (BAS) from floristically rich plots (TSPE) with many small trees (ONE, TREE). Principal component 2 (17.3% of the variance) represented a vine and shrub element separating plots with high and low counts of species (VSPE, SSPE) and stems (VINE, SHRU). Principal component 3 (13.3% of the variance) exhibited positive loadings for large trees (SIX) and basal area (BAS), variables which also figured prominently on the first component. Although factor scores differed significantly among localities (Kruskal-Wallis ANOVA of locality medians; PC 1: $\chi^2 = 19.90$, df = 4, $P = 0.001$; PC 2: $\chi^2 = 26.19$, df = 4, $P < 0.001$; PC 3: $\chi^2 = 14.32$, df = 4, $P = 0.006$), the overlap of concentration ellipses surrounding factor scores indicated that intralocality variability accounted for much of the observed variation.

DISCUSSION

Understory stem density in early successional floodplain forest in the southeastern United States frequently exceeds 200,000 stems/ha (GRG unpubl. data). However, the maximum count of stems (SHRU + CANE) observed on Swainson's Warbler territories in the core breeding range (104,710 stems/ha) and in the Great Dismal Swamp, southeastern Virginia (81,400 stems/ha; Graves 2001), was about half that value. These data indicate that habitat quality is not linearly correlated with the abundance of small woody stems. Instead,

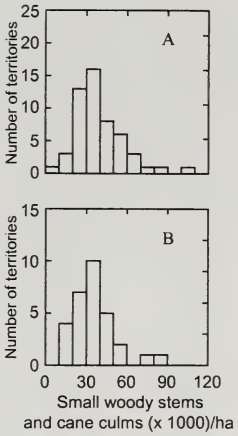

FIG. 3. Density of small woody stems and cane culms in territories of the Swainson's Warbler: (A) pooled data from five study sites in the core breeding range reported in this paper, and (B) data from the Great Dismal Swamp, southeastern Virginia (Graves 2001).

a relatively narrow range of stem densities (ca 30,000–50,000 stems/ha) appears to provide high quality cover for nesting and foraging throughout its breeding range (Table 1). Counts of understory stems (SHRU + CANE) pooled across the five study sites in the core breeding range (n = 53 territories, median = 34,773 stems/ha; Table 1) were not statistically different (Kruskal-Wallis ANOVA, χ^2 = 0.73, df = 1, P = 0.39) from comparable data collected with identical sampling techniques in the Great Dismal Swamp (n = 30 territories; median = 36,220 stems/ha; Fig. 3). Investigations at other locations reported a wider range of mean stem densities on breeding territories: southern Illinois (small woody stems and cane: mean = 26,390 stems/ha; Eddleman et al. 1980); southern Missouri (cane: mean = 61,000 culms/ha; Thomas et al. 1996); central Georgia (cane: mean = ca 50,000 culms/ha; Meanley 1966); and South Carolina (small woody stems: mean = 99,836 stems/ha; Hamel 1981). I suspect that a significant fraction of this variation may be attributed to marked differences in vegetation sampling techniques. The apparent absence of giant cane in the Whiskey Bay corridor, perhaps the premier Swainson's Warbler locality in terms of total breeding population, should put to rest the hypothesis first proposed by Brewster (1885) that cane is an essential component of prime habitat.

Contemporary management strategies for the Swainson's Warbler call for the preservation of large blocks of unfragmented forest (Eddleman et al. 1980, Hunter et al. 1994, Mueller et al. 2000), the maintenance and regeneration of canebrakes (Eddleman et al. 1980, Thomas et al. 1996), the creation of small canopy gaps by selective cutting (Eddleman et al. 1980, Pashley and Barrow 1993), and the generation of larger (≤1.6 ha) gaps through clearcutting (Eddleman et al. 1980). On the other hand, Dickson et al. (1993) suggested that populations would benefit by setting aside mature floodplain forests and allowing young stands of trees to mature. As previously suggested (Graves 2001), data from the core breeding range support the hypothesis that Swainson's Warblers prefer early successional forest in the current landscape or disturbance gaps in old growth forest.

In the remainder of this paper I discuss some aspects of habitat management for the Swainson's Warbler. First, the hydroperiod of reserves managed for this species must be compatible with the warbler's terrestrial foraging behavior (Graves 2001). Breeding territories are restricted to moist soils, but flooding is a potent determinant of habitat occupancy patterns on local and regional scales (Meanley 1966, 1971; Graves 2001). Ideally, water levels should be maintained at or below ground level from late March through September. Furthermore, annual winter and spring flooding should not be so intense as to scour and wash away the accumulated bank of leaf litter and detritus, which constitutes the critical foraging substrate on the breeding and wintering grounds (Meanley 1970; Graves 1996, 1998, 2001; Strong 2000). It is unfortunate that a substantial fraction of the remaining tracts of floodplain forest on the coastal plain and in the lower Mississippi Valley (see map in Twedt and Loesch 1999) is subject to annual flooding during the breeding season. In essence, the calculation of effective area of Swainson's Warbler reserves should begin with the subtraction of chronically flooded zones.

Although the area requirements for viable breeding populations of Swainson's Warblers are believed to be substantial owing to its

FIG. 4. Physiognomic profile of habitat elements typically associated with breeding territories of the Swainson's Warbler in its core breeding range: (A) vine "tents" and tangles; (B) small shaded glades carpeted with leaf litter; and (C) thickets of shrubs, tree saplings, vines, and *Rubus* spp. associated with canopy gaps. Giant cane (D) is rare or absent from many prime breeding sites in the lower Mississippi Valley.

large territory size and relatively low population density (Eddleman et al. 1980, Brown and Dickson 1994, Hunter et al. 1994), the degree to which it tolerates forest fragmentation is unknown. Estimated population densities reported in this paper ranged from 3.8–20.5 males/km^2. The latter figure represented the highest density estimate obtained with standardized censuses along linear transects >3.5 km in length (GRG unpubl. data). Densities of 5–8 pairs/km^2 are perhaps attainable in multipurpose floodplain reserves. Using this range of density values as a guideline, reserves capable of supporting 500 pairs of Swainson's Warblers would vary in size from 6,250–10,000 ha, or approximately 2.78–4.44 times larger than the minimum area requirement suggested by Hunter et al. (1994).

The dense breeding populations (10–20 territorial males/km^2) of Swainson's Warblers encountered at Whiskey Bay and Pearl River occurred in successional floodplain forest dominated by small (<25 cm dbh) trees (ca 620–820 stems/ha) and understory thickets (ca 35,000–48,000 small woody stems/ha). In these localities and many others across the warbler's breeding range (Eddleman et al. 1980, Brown and Dickson 1994, Thomas et al. 1996, Graves 2001), canopy height, basal area, and floristics appear to be relatively unimportant factors in habitat selection, provided that understory requisites are met—which explains the warbler's occurrence in regenerating clearcuts as well as in old growth forest. Breeding density is far lower (typically <2.0 males/km^2) in taller, more mature forests characterized by a closed canopy and relatively sparse undergrowth (<10,000 small woody stems/ha; GRG unpubl. data). Territories in such habitat typically are centered at large disturbance gaps dominated by luxuriant thickets of tree saplings, shrubs, and woody vines (Fig. 4).

The attractiveness of closed canopy forests to Swainson's Warblers can be enhanced by selective thinning or the creation of small clearcuts (Eddleman et al. 1980, Pashley and Barrow 1993). Selective thinning, to the extent needed to simulate optimal habitat, may be logistically unfeasible and too labor intensive to be uniformly applied to large (ca 5,000–10,000 ha) reserves of maturing secondary forest. The generation of small clearcuts, spatially configured to serve as territorial nuclei, may be a more practical management alternative. The optimal size of clearcuts will depend upon the overall quality of the habitat. Experimental evidence from the Great Dismal Swamp suggests that clearcuts as small as 0.25 ha (at a density of 25 clearcuts/km^2) may induce Swainson's Warblers to colonize marginal habitat (GRG unpubl. data). Larger (0.5–

1.0 ha) clearcuts may be more effective attractors, but a variety of cutting and thinning protocols is likely to yield satisfactory outcomes.

Habitat management on agroforestry lands in the southeastern United States requires a different strategy, however, especially with the proliferation of high capacity wood chip mills, which encourage large scale clearcutting of young deciduous forests (trees as small as 7.5 cm dbh) for pulp. The possibility that the Swainson's Warbler may not perceive agroforestry landscapes as excessively fragmented is suggested by the documented occurrence of breeding in regenerating clearcuts (Eddleman et al. 1980, Brown and Dickson 1994, Peters 1999), young pine plantations (Carrie 1996, Bassett 2001, GRG unpubl. data) and large disturbance gaps in mature forests (GRG unpubl. data). In fact, mosaics of regenerating clearcuts (6–30 years old) frequently support robust breeding populations (Peters 1999; GRG unpubl. data). To facilitate colonization and occupancy of agroforestry lands on floodplains, pulpwood producers should be encouraged to make relatively small (10–20 ha) clearcuts on a staggered 25-year cutting rotation.

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WINTER ABUNDANCE OF AND HABITAT USE BY HENSLOW'S SPARROWS IN LOUISIANA

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ABSTRACT.—Population trend data indicates the Henslow's Sparrow (*Ammodramus henslowii*) is declining. Little information is available on the status, distribution, and habitat requirements of this species during winter. We obtained winter density estimates of Henslow's Sparrows and quantified and compared habitat structure along transects occupied and unoccupied by birds in longleaf pine (*Pinus palustris*) forests in westcentral Louisiana. We flushed Henslow's Sparrows from 14 transects during four surveys of 48 20- × 100-m transects from January to February 1996, and 20 transects during four surveys of 46 of the same transects from December 1996 to February 1997. The range of Henslow's Sparrow densities for both survey periods combined was 0.0–13.8 birds/ha (median = 0.0, 75th percentile = 1.3, 95th percentile = 5.0). We used logistic regression to evaluate the association of vegetative structure with Henslow's Sparrow habitat use. The most parsimonious model included litter depth and herbaceous cover as habitat variables predictive of Henslow's Sparrow occurrence. The model correctly classified the occupancy status of 79% (52 of 66) of observed transects. The number of Henslow's Sparrows observed in transect surveys declined with increased number of growing seasons since the last burn, suggesting fire may influence habitat quality. *Received 17 July 2000, accepted 15 May 2002.*

The Henslow's Sparrow (*Ammodramus henslowii*) is a grassland species that breeds in the northeastern and northcentral United States and southern Canada, and winters in the southeastern United States (Hands et al. 1989, Butcher and Lowe 1990). Breeding Bird Survey (BBS) data show a significant decline between 1966 and 1994 (Peterjohn et al. 1994). Several researchers have expressed concern regarding recent declines on its breeding ground (Hands et al. 1989, Herkert 1994, Tate 1986, Pruitt 1996). The Henslow's Sparrow is listed as endangered in Canada and as either endangered, threatened, or a species of concern in 16 states in the U.S. (Pruitt 1996).

Few reliable estimates of winter abundance are available for Henslow's Sparrows. Currently, data from Christmas Bird Counts (CBC) provide the only winter population data for Henslow's Sparrows. The relatively secretive behavior of Henslow's Sparrows during winter reduces the likelihood of detection by observers during CBCs. In addition, statistical methods for rigorous analysis of CBC data are not yet available. Consequently, CBC data probably are not reliable for assessing winter Henslow's Sparrow population numbers (Butcher and Lowe 1990).

There is little information on the winter habitat of Henslow's Sparrows. Winter habitats have been described generally as open pine forests with a grass understory and wet meadows of the southeastern coastal plain (Hunter 1990, Hamel 1992). Most of the longleaf pine (*Pinus palustris*) forests of the southeastern coastal plain of the U.S. have been harvested and replanted with other pine species (Frost et al. 1986). Fire suppression in many of the remaining longleaf pine forests has resulted in the reduction or elimination of the herbaceous understory of this fire climax community (Frost et al. 1986, Bridges and Orzell 1989). The impact of these habitat alterations on the Henslow's Sparrows and the relative importance of this habitat for wintering populations of this species are unknown.

The purpose of our study was to provide density estimates of Henslow's Sparrows in longleaf pine forests during winter and to quantify the habitat structure of occupied sites. We predicted that within the longleaf pine landscape, occupied habitat would differ structurally from unoccupied habitat at a local scale.

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METHODS

Study site.—We surveyed for Henslow's Sparrows on the 13,335-ha Peason Ridge training area of Fort Polk (31° 21′ N, 93° 14′ W) and the 16,188-ha Vernon Ranger District (31° 01′ N, 93° 13′ W) of the Kisatchie National Forest, Louisiana. The area is characterized by flat to gently rolling plains with moderate slopes (1–3%) and well-drained fine sandy loam soils (Daigle et al. 1989). Vegetation consisted of a longleaf pine overstory and a grass understory comprised mostly of *Schizachrium* spp., *Andropogon* spp., *Panicum* spp., and *Dicanthelium* spp. Both areas were managed for timber production on a 120-year rotation and were prescribed burned at 3-year intervals.

Surveys.—We established 48 20- × 100-m transects spaced approximately 0.5 km apart in mature longleaf pine habitat. Transects at 0.5-km intervals that would have fallen in habitats other than mature longleaf pine forest were relocated to the nearest adjacent area of this habitat type. We surveyed each transect four times from January to February 1996 (first survey period) and 46 of 48 transects four times from December 1996 to February 1997 (second survey period). We conducted surveys from 08:00–12:00 on days when wind speeds were <2 m/s, skies were clear to partly cloudy, and daytime temperatures were >10° C. Survey crews included two individuals spaced approximately 12 m apart, each using two 4-m bamboo cane poles to beat the vegetation to flush birds. An observer centered between the two pole operators recorded birds as they flushed in front of the 20-m wide survey line. After flushing, birds were monitored until they landed to ensure that they were not counted more than once. Nearly all birds that we flushed flew beyond the transect, but not to an adjacent transect.

To estimate bird density for each transect, we divided the mean number of birds counted on the four surveys by the area of the transect (0.2 ha). We used these density estimates for the 48 transects to calculate the overall median, 75th, and 95th percentiles, and range for each annual survey period and for both periods combined.

Habitat measurements.—We sampled vegetation on occupied transects using 0.04-ha circular plots centered on the point where a bird was flushed. We measured vegetation during March or April following both survey periods to minimize disturbance of birds occupying the transects. We measured overstory density with a spherical densiometer (Nuttle 1997) and tree basal area with a 1-factor metric prism. We recorded the number of trees <25 cm dbh and >2 m tall (midstory layer) and the number of trees >25 cm dbh (overstory layer). Woody stems <1 cm dbh and <2 m tall were considered shrubs. We measured standing herbaceous vegetation using a 1-m rod held perpendicular to the ground to count the number of grass blades and forbs contacting the rod at a height of 0–100 cm. Ten separate counts of herbaceous vegetation were made approximately every 2 m with the rod along a line transect centered across the plot and oriented toward the north. We measured litter depth, defined as the vertical distance between the soil and the top surface of the accumulated leaf litter and matted dead grass, at the same points herbaceous cover was measured. We collected the same vegetative measurements at randomly selected points within transects where birds were not detected during the survey period to represent available unoccupied habitat.

Statistical analysis.—We calculated mean vegetation measurements by averaging data collected from all sampled points within each transect-survey period. We transformed litter depth measurements to a standard normal distribution to remove the effect of a systematic difference in its measurement between survey periods. We categorized transects as used if at least one bird was flushed during the survey period. We determined correlation coefficients among vegetation measurements.

We used model selection to analyze habitat use. Based on prior field observations, at the start of this study we selected habitat variables to measure in the field that we believed would be important correlates of habitat use. Using univariate logistic regression (Hosmer and Lemeshow 1989), we analyzed the importance of each independent variable (vegetative measurements and survey period) with respect to transect use. We ranked the relative weight of each independent variable using the small sample correction of Akaike information criterion (AIC_c; Burnham and Anderson 1998). We then constructed a global multivariate logistic regression model that included all variables except those that were highly correlated ($r > 0.7$) and explained a similar biological phenomenon, selecting the variable with the lowest AIC_c from the correlated set for inclusion in the model. We tested the fit of the global model based on deviance and a significance level of 0.40, and a visual examination of observed and fitted values and residuals (Agresti 1996, Venables and Ripley 1999). We used stepwise selection (stepAIC; Venables and Ripley 1999) to select the most parsimonious model based on minimizing AIC (Burnham and Anderson 1998). We calculated model uncertainty in terms of Akaike weights, which indicate the likelihood of the model for a given set of data (Burnham and Anderson 1998). We developed correct classification and sensitivity scores for the AIC_c-selected model to assess model performance. Correct classification is the percent of all observations that were correctly classified; sensitivity is the ability to correctly predict use only (Fielding and Bell 1997).

After examining habitat use, we suspected that there was a relationship between time since a transect was burned and the density of Henslow's Sparrows. To investigate this relationship, we obtained the fire history for each transect from fire management records maintained by the Fort Polk environmental division and the U.S. Forest Service. These records enabled us to categorize 66 of the 96 transects into one of three categories: transects with one growing season, transects with 2 growing seasons, and transects with >2 growing seasons since last burned. We tested the association

TABLE 1. Density (birds/ha) of Henslow's Sparrows (*Ammodramus henslowii*) from transect surveys in longleaf pine forests in westcentral Louisiana.

Period	Number of transects with ≥1 bird flushed[a]	Number of birds flushed[b]	Density[c]			
			Median	75th percentile	95th percentile	Range
Jan. 1996 to Feb. 1996	14 (48)	35	0.0	1.3	5.0	0.0–13.8
Dec. 1996 to Feb. 1997	20 (46)	33	0.0	1.3	2.5	0.0–8.8
Total	34 (94)	68	0.0	1.3	5.0	0.0–13.8

[a] Number of transects surveyed in parentheses.
[b] Total number of birds flushed during four surveys per survey period.
[c] Number of birds per hectare calculated from the mean number of birds per hectare for each of the 48 transects.

between the three growing season categories and the number of birds per transect with Pearson's chi-square tests. All analyses were conducted using S-Plus 2000 (MathSoft 1999).

RESULTS

We detected Henslow's Sparrows on 58% (28 of 48) of transects over the two survey periods (Table 1). Two transects that burned in August 1996 had no herbaceous cover that could support birds during the second survey period and consequently were not surveyed. Forty-three percent (6 of 14) of transects occupied by birds the first survey period were occupied the second survey period. No birds were detected on 71% (34 of 48) of transects during the first survey period and 57% (26 of 46) of transects during the second survey period.

Habitat characteristics were measured in 13 occupied and 17 unoccupied transects the first survey period and 19 occupied and 17 unoccupied transects the second survey period. Transformed litter depth, basal area, and herbaceous cover were the most important variables in determining transect use (Table 2). Basal area, overstory density, and trees >25 cm dbh were highly correlated and explain the same biological phenomenon. Since basal area had the lowest AIC_c value, it was entered into the global model. The other variables appeared to have little association with habitat use. The global model exhibited no evidence of lack-of-fit. The best model for discriminating between used and unused transects included litter depth (parameter estimate $\beta = 0.56$, SE = 0.19) and herbaceous cover (parameter estimate $\beta = -2.01$, SE = 0.53; Table 3). This model received >50% of the Akaike weight and was more than twice as likely to be the best model. This model correctly classified the occupancy status of 79% (52 of 66) of observed transects, with a 78% sensitivity rate (correctly classifying 25 of 32 used transects). The model indicates that the probability of use

TABLE 2. Mean values for vegetative measurements collected in 0.04-ha plots within transects that were used and unused by Henslow's Sparrows (*Ammodramus henslowii*) in longleaf pine forests in westcentral Louisiana, January to February 1996 and December 1996 to February 1997. Parameter estimates, *P* values for *t*-statistics, and bias-corrected Akaike Information Criterion (AIC_c) are presented from the global logistic regression model.

Variable	Occupied		Unoccupied		Parameter estimate	SE	*P*	AIC_c
	$\bar{x}$	SE	$\bar{x}$	SE				
Litter depth (cm)[a]	−0.41	0.11	0.49	0.17	−2.03	0.57	<0.001	77.30
Basal area (m^2/ha)	7.58	0.89	10.90	0.89	−0.06	0.07	0.222	88.69
Herbaceous cover (contacts/m)	4.97	0.40	3.89	0.27	0.53	0.23	0.012	90.13
Shrub density (stems/m^2)	114.81	23.37	77.46	13.49	0.00	0.00	0.493	93.61
Survey period	—	—	—	—	−0.01	0.35	0.488	95.04
Trees <25 cm dbh (stems/ha)	4.95	1.18	5.00	1.28	0.05	0.06	0.192	95.62
Overstory density (%)[b]	47.31	5.24	61.81	2.68	—	—	—	89.51
Tree >25 cm dbh (stems/ha)[b]	2.69	0.50	4.19	0.41	—	—	—	90.11

[a] Transformed to a standard normal distribution.
[b] Variables not included in the logistic regression model to avoid collinearity with basal area.

TABLE 3. Habitat models used to explain differences between transects occupied and unoccupied by Henslow's Sparrows (*Ammodramus henslowii*) in longleaf pine forests in westcentral Louisiana, January to February 1996 and December 1996 to February 1997. The bias-corrected Akaike Information Criteria (AIC_c), the difference in AIC_c values between the *i*th model and the lowest AIC_c value (Δ_i), and Akaike weights (w_i) are presented for the set of models considered in the stepwise model selection process.

Variable	Deviance	AIC_c	Δ_i	w_i
Herbaceous cover, litter depth[a]	61.721	68.11	0	0.56
Herbaceous cover, trees <25 cm dbh, litter depth	60.912	69.57	1.46	0.27
Herbaceous cover, trees <25 cm dbh, basal area, litter depth	60.193	71.19	3.08	0.12
Year, herbaceous cover, trees <25 cm dbh, basal area, litter depth	60.192	73.62	5.51	0.04
Year, herbaceous cover, trees <25 cm dbh, shrub density, basal area, litter depth	60.192	76.12	8.01	0.01

[a] Transformed to a standard normal distribution.

increased as litter depth decreased and herbaceous cover increased.

We found a marginally significant negative association between the number of Henslow's Sparrows observed on transects and the number of growing seasons since last burned (Fig. 1).

DISCUSSION

Henslow's Sparrows on our study area used sites with little or no litter and large amounts of herbaceous cover. In our study area, such habitat conditions occurred in open pine savannahs and openings in extensive forest. Large expanses of sparsely forested grassland were common on Fort Polk as a result of previous military use, frequent wildfires, and prescribed burns. Forest openings occupied by sparrows often were the result of trees that had been killed by insect infestations or wind. Fewer trees prevent rapid accumulations of litter and allow greater light penetration in the herbaceous understory, maintaining the habitat structure used by Henslow's Sparrows.

Wintering Henslow's Sparrows used sites in our study area without the deep accumulations of surface litter typical of sites used during the breeding season. On the breeding grounds, this species generally is found on sites with a well-developed litter layer that they use for

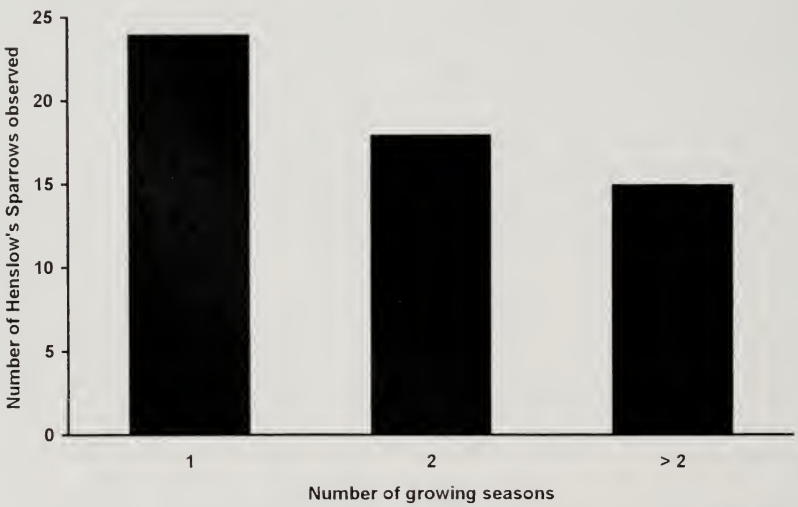

FIG. 1. The number of Henslow's Sparrows observed in longleaf pine forests was negatively related to the number of seasons since last burned (χ^2 = 5.23, 2 = df, P = 0.073). Data are from four surveys of 48 20- × 100-m transects from January to February 1996, and four surveys of 46 of those transects from December 1996 to February 1997, westcentral Louisiana.

nesting, escaping from predators, and foraging (Wiens 1969, Robins 1971, Kahl et al. 1985, Zimmerman 1988, Hanson 1994, Herkert 1994). Anecdotal accounts suggest that during the winter, Henslow's Sparrows feed mostly on seeds picked from the ground (Oberholser 1974). Foraging may be most efficient for birds that use areas with little or no litter where seeds on the ground are easily accessible. In addition, the accumulation of dead vegetation and litter after each growing season may depress herbaceous growth during following years (NRC pers. obs.). Birds typically run across the ground rather than fly when pursued (NRC pers. obs.). The lack of surface litter may provide a more open substrate for the birds as they move across the ground.

Fire may influence habitat suitability for wintering Henslow's Sparrows by reducing litter and maintaining the herbaceous understory. Burning can increase the richness and coverage of herbaceous plants, depending upon the season and frequency an area is burned (White et al. 1991). Prescribed burns on Fort Polk and the Vernon Ranger District were conducted during fall and winter (September to March). White et al. (1991) found that herbaceous species richness was significantly higher for winter burn treatments than for nonburn treatments. Hodgkins (1958) also found that forb cover increased during the first growing season after a fire and decreased during subsequent years as grass and woody cover increased. The availability of forbs during winter may influence the suitability of habitat for Henslow's Sparrows. We detected more sparrows on transects located in areas that had undergone at least one growing season since the last burn, and the number of sparrows declined as the number of growing seasons increased. Plentovich et al. (1999) also found large numbers of Henslow's Sparrows in recently burned areas that had high densities of herbaceous vegetation. Reducing the frequency of fires may adversely impact Henslow's Sparrow winter habitat quality in longleaf pine communities by allowing dead vegetation and litter to accumulate in the herbaceous understory.

The presence or absence of low woody vegetation was not a significant predictor of occupancy in our study area, although encroachment by low woody vegetation can limit use by Henslow's Sparrows on their breeding grounds (Zimmerman 1988). Low (<1 m) shrub clumps were present in low numbers throughout the understory of both occupied and unoccupied sites in our study area. Birds often flew into shrubs after flushing during our surveys, suggesting that widely spaced shrubs may be important as cover. Transects had been routinely burned every 3 years, promoting growth of the herbaceous vegetation and limiting woody encroachment. Extensive shrub cover can reduce the amount of herbaceous cover (Frost et al. 1986, Bridges and Orzell 1989) and may ultimately reduce winter habitat quality for Henslow's Sparrows.

Sites where Henslow's Sparrows overwinter in our study area generally were drier than the winter habitat described by Plentovich et al. (1999). The herbaceous understory in transects in our study area occurred exclusively on dry, well-drained sandy loam soils. In contrast, Plentovich et al. (1999) found Henslow's Sparrows to occur in areas with moist soils either in pitcher plant (*Sarracenia* spp.) bogs or in transition areas between pitcher plant bogs and drier upland habitats. Large numbers of Henslow's Sparrows also have been found in moist grasslands and bogs in coastal Mississippi (M. S. Woodrey unpubl. data). Although the soil moisture level was substantially different in our study area compared to these other areas, all areas appeared to have the well-developed herbaceous understories that the species seems to prefer.

The importance of a well-developed herbaceous layer suggests that grassland habitats other than those associated with the longleaf pine community should be surveyed for Henslow's Sparrows. Abandoned agricultural fields, easements along powerlines and roads, and forest openings produced by both even-age (clearcuts, shelterwood cuts) and uneven-age (group selection cuts) management practices should be studied to determine whether such areas provide suitable winter habitat for Henslow's Sparrows.

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SPATIAL AND HABITAT RELATIONSHIPS OF RED-EYED AND BLUE-HEADED VIREOS IN THE SOUTHERN APPALACHIANS

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ABSTRACT.—Red-eyed (*Vireo olivaceus*) and Blue-headed (*V. solitarius*) vireos have similar foraging ecologies, similar songs, and occupy similar forest habitats. Evidence suggests, however, that the typical pattern of habitat and foraging segregation in sympatric vireos may not be observed in the southern part of their range of sympatry. We tested the degree of ecological overlap in the southern Appalachians of Virginia by asking whether these species segregate via interspecific territoriality or habitat use. We quantified response to heterospecific song, territory overlap, and habitat characteristics during the breeding seasons of 1997 and 1998. Red-eyed and Blue-headed vireos responded at low frequencies (9% and 2%, respectively; years combined) to the songs of the other species. Not surprisingly, given the playback results, approximately 54% of territories examined for each species overlapped with a territory of the other species. Within territories, both vireos used structurally similar habitat. Microhabitat composition, however, differed between species. Blue-headed Vireos occurred in areas with greater abundance of white oaks (*Quercus* spp.), conifers, and snags, whereas Red-eyed Vireo habitat had qualitatively greater abundance of red oaks and red maples (*Acer rubrum*). Red-eyed and Blue-headed vireo habitat was discriminated further by the presence of striped maple (*A. pensylvanicum*) and black locust (*Robinia pseudoacacia*) in the canopy of Red-eyed Vireo habitat, whereas conifers and black birch (*Betula lenta*) were more common at sites where Blue-headed Vireos were observed. Shrub species composition did not differ significantly between vireo habitats. Red-eyed and Blue-headed vireos showed only subtle habitat segregation at our study site in the southern Appalachians, and we found little evidence of interspecific aggression. *Received 6 June 2001, accepted 3 February 2002.*

The study of avian niche relationships provides information about patterns of segregation among coexisting species that is prerequisite to identifying the ecological mechanisms structuring avian communities. Birds of the genus *Vireo* provide a good system for studying niche overlap because species pairs interact in different combinations in different settings. Vireos show considerable dietary overlap (Chapin 1925) and they are broadly sympatric (Price et al. 1995), but they rarely coexist within a habitat (Hamilton 1958, 1962; Cody 1985). When vireos do share habitat, they typically show either horizontal or vertical segregation into different microhabitats (Hamilton 1958, 1962) and often differ in body size (Cody 1985). Such consistent patterns of segregation in various species pairs has been interpreted as evidence for the importance of competition in vireos (Hamilton 1962, Cody 1985). However, some assemblages of vireos do not conform to these patterns, and their ecological relationships may be particularly instructive.

For example, Red-eyed (*Vireo olivaceus*) and Blue-headed (*V. s. solitarius*) vireos are similar in size (15.0–17.0 g) and widely sympatric in the forests of Canada and the eastern United States during the breeding season (Price et al. 1995). Over most of this area of sympatry, the two species have similar foraging ecology (Chapin 1925, Williamson 1971, Holmes et al. 1979, Robinson and Holmes 1982) but occupy distinct habitats. Red-eyed Vireos typically inhabit well-developed, deciduous forests (Bent 1950, Hamilton 1962, James 1971) with some shrub understory (James 1971), whereas Blue-headed Vireos inhabit middle-aged to mature evergreen forests with sparse understory (James 1998) or mixed deciduous-coniferous forests (Bent 1950, Hamilton 1962). This pattern, exhibited in the northern part of the range of sympatry, is typical of vireos, but it appears to break down between these species in areas of sympatry in the southern Appalachians where Red-eyed Vireos coexist with a subspecies of Blue-headed Vireo (*V. s. alticola*, hereafter Blue-headed Vireo). Our observations suggest that there is considerable overlap in habitat use between Red-eyed and Blue-headed vireos

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in the southern Appalachians, and available information (Rabenold 1978, Petit et al. 1990) suggests that these two species may be more similar in foraging ecology in this region as well. However, no studies have quantified the interactions between these species in the southern Appalachians.

The objective of this research was to quantify ecological factors potentially influencing coexistence between these two species in the southern Appalachians at the level of horizontal habitat segregation. In this study we considered the potential for interspecific aggression by determining if Red-eyed and Blue-headed vireos responded to playback of songs of the other species or held mutually exclusive territories. We also quantified habitat characteristics to determine if Red-eyed and Blue-headed vireos used different microhabitats within the available habitat.

STUDY AREAS AND METHODS

Study areas.—We conducted this research from 12 June to 16 July 1997 and 17 April to 15 June 1998 at the Univ. of Virginia's Mountain Lake Biological Station (MLBS) and adjacent Jefferson National Forest in Giles County, Virginia (37° 22′ N, 80° 32′ W; elevation 1,160 m at MLBS). MLBS is located on Salt Pond Mountain in the Appalachian Mountains of southwestern Virginia. The forest canopy included red oaks (*Quercus coccinea*, *Q. rubra*, and *Q. velutina*), white oaks (*Q. alba* and *Q. montana*), maples (*Acer rubrum* and *A. saccharum*), hickories (*Carya glabra*, *C. ovata*, and *C. tomentosa*), birches (*Betula alleghaniensis* and *B. lenta*), American beech (*Fagus grandifolia*), and yellow poplar (*Liriodendron tulipifera*). Scattered conifers intermingled with deciduous trees included pines (*Pinus strobus* and *P. rigida*), hemlocks (*Tsuga canadensis* and *T. caroliniana*), and red spruce (*Picea rubens*). Representative shrubs included striped maple (*A. pensylvanicum*), witch-hazel (*Hamamelis virginiana*), rhododendron (*Rhododendron maximum*), mountain-laurel (*Kalmia latifolia*), red maple, serviceberry (*Amelanchier arborea*), and American chestnut (*Castanea dentata*).

Recording songs.—We recorded songs of Red-eyed and Blue-headed vireos on Butt Mountain (located approximately 9 km southwest of MLBS) to ensure that playback experiments were conducted using songs representing the local dialect of each species (Kroodsma 1986, 1989). We recorded Blue-headed Vireo songs (n = 5) from 2 to 4 May 1997 and Red-eyed Vireo songs (n = 5) from 30 May to 1 June 1997. Recordings were made on Sony High Fidelity (Type I, normal bias) cassette tapes using a Marantz PMD-430 tape recorder and a Sennheiser ME66 shotgun microphone equipped with a K6C power supply, MZS-6 shock mount, and a MZW-66 windscreen (Saul Mineroff Electronics, New York). We transferred recordings containing at least 60 consecutive seconds of song (i.e., recordings were not spliced together) to TDK 1M 1-min loop cassettes using a Sony CFD-545 dual cassette dubbing system. One-min loop tapes of five different individuals of each species were made for use in playback experiments.

Playback experiments.—We conducted playbacks at 200-m intervals along 20 parallel 1-km transects along Virginia St. Rt. 613 beginning 0.5 km north of MLBS. Transects were separated by 200 m. Because our emphasis in this study was to determine how interspecific interactions might affect habitat use, we chose to conduct playbacks along transects (as opposed to within known territories). This approach allowed us to estimate the frequency with which interspecific aggression is likely to impinge on site selection over the habitat as a whole. During 1997, we conducted playback experiments from 12 June to 13 July, a period coinciding with late incubation through nestling and fledgling stages of the breeding season (James 1998, Cimprich et al. 2000). During 1998, we conducted playbacks from 8 May to 2 June, a period coinciding with territory establishment, nest initiation, and early incubation (James 1998, Cimprich et al. 2000). All experiments were conducted between 05:00 and 10:30 (EST) to minimize time-of-day effects. Different transects were established each year so that no site was used more than once for playbacks.

We conducted each 6-min playback trial in two 3-min periods (Rice 1978a). During the pretrial period (first 3 min), we noted all Red-eyed and Blue-headed vireos heard (song or call) or seen in order to estimate the relative abundance of each species. During the trial period (second 3 min), we broadcast a randomly selected song tape using a Radio Shack CTR-96 handheld tape recorder (volume setting 7) equipped with a Realistic 10A2 speaker set at maximum volume. Individuals were considered to be responding to playback if they approached the playback area (≤10 m of the speaker) and appeared to search for the source of the song. Although responses to song playback may be graded (e.g., increased song rate with no approach to the playback speaker), and we did detect graded responses to conspecific playback in both species, we did not detect graded responses to heterospecific playback in either species (SPH and CRC unpubl. data). Thus, we chose the above discrete measure of response for our analyses. We conducted 61 playback trials (28 of Blue-headed Vireos and 33 of Red-eyed Vireos) during 1997 and 59 playback trials (28 of Blue-headed Vireos and 31 of Red-eyed Vireos) during 1998.

Territory mapping.—We mapped Red-eyed and Blue-headed vireo territories in a 36-ha area (gridded at 50-m intervals) centered around MLBS (about 0.5 km south of the playback areas) following the recommendations of Bibby et al. (1993). Once or twice weekly, we walked a route passing ≤50 m of each point within the territory mapping area and recorded each Red-eyed or Blue-headed vireo located visually or audibly on a census map to the nearest 10 m. An

unmarked map was used during each visit to reduce bias from previous registrations. Data were compiled on a composite territory map at the end of each field season and territories were determined following the recommendations of Bibby et al. (1993:50–53).

Habitat characteristics.—We selected plots to quantify habitat characteristics within territories of Red-eyed (n = 43) and Blue-headed (n = 32) vireos throughout the study site (mapping and playback areas). One plot per territory was centered on a tree where Red-eyed or Blue-headed vireos were observed singing and foraging. An 11.3-m radius plot was established around each plot center and habitat characteristics were quantified (James and Shugart 1970, James 1971). All trees (woody stems ≥10 cm dbh) were identified and dbh was recorded. Shrubs (woody stems ≥1.4 m tall and <10 cm dbh) were quantified along four 11.3- × 1.5-m transects along the cardinal directions of a compass, and canopy cover was estimated at 13 points (one center point and four points along each transect; points were approximately 2.5 m apart) within each plot.

Data analysis.—We examined playback response data using analysis of frequencies (G-test) to determine if Red-eyed and Blue-headed vireos differed in their likelihood to respond to playback of conspecific and heterospecific song during each year. We assessed whether Red-eyed and Blue-headed vireo habitats differed in (1) overall structure as described by number of trees and shrubs, basal area, and canopy cover; (2) tree species composition; or (3) shrub species composition. Our approach was to carry out univariate comparisons of the individual variables followed by MANOVA of all the variables describing a particular habitat feature (structure, tree composition, shrub composition). Univariate comparisons of Red-eyed and Blue-headed vireo habitat features were made using t-tests (when the parametric assumptions of normality and homoscedasticity were met) and a Wilcoxon two-sample test (when the parametric assumption of normality was not met). In cases where MANOVA indicated a significant difference between species, we used a canonical discriminant analysis to identify the variables that best discriminated Red-eyed and Blue-headed vireo habitat.

We pooled the habitat data from both years. We included in the tree species analysis only those species or species groups that occurred at a frequency of ≥13 individuals in the total sample: REDOAK (red oaks, comprising *Quercus coccinea*, *Q. rubra*, and *Q. velutina*; 32% of trees sampled), REDMAP (red maple; 21%), WHTOAK (white oaks, comprising *Q. montana* and *Q. alba*; 12%), SNAG (standing dead trees; 12%), CONFER (conifers, comprising *T. canadensis*, *Pinus strobus*, and *P. rigida*; 5%), BLKGUM (black gum, *Nyssa sylvatica*; 5%), SRVBER (service berry; 3%), BLKBIR (black birch, *Betula lenta*; 3%), HICKY (hickories, comprising *Carya cordiformis*, *C. glabra*, *C. ovata*, and *C. tomentosa*; 2%), BLKCHY (black cherry, *Prunus serotina*; 1%), YELBIR (yellow birch, *B. allegheniensis*; 1%), CUCTRE (cucumber magnolia, *Magnolia acuminata*; 1%), STRMAP (striped maple; 0.7%), ABEECH (American beech; 0.6%), and BLKLOC (black locust; 0.6%).

We included in the shrub species analysis only those species or species groups that occurred at a frequency of ≥11 individuals in the data set: STRMAP (37%), WITHAZ (witch-hazel; 17%), AMCNUT (American chestnut; 7%), SRVBER (6%), KALMIA (mountain-laurel; 6%), SNAG (6%), REDMAP (4%), CONFER (3%), RHODOD (rhododendron; 3%), VACCIN (*Vaccinium* spp.; 3%), and BLKGUM (2%).

We used Dunn-Sidák correction for multiple inferences (Sokal and Rohlf 1995:241) to hold experimentwise error at $\alpha = 0.05$ for each family of *a priori* tests. A family of tests is defined as all comparisons falling under the same general null hypothesis (Chandler 1995). For example, the overall comparison of Red-eyed and Blue-headed vireo responses to conspecific song comprised four tests of the null hypothesis that Red-eyed and Blue-headed vireos respond similarly to their own species song. Similarly, heterospecific playback experiments comprised five tests and habitat characteristics comprised seven tests. P values of standard analyses were ordered from smallest to largest to determine significance by the Dunn-Sidák correction. The comparison with the smallest P value was considered significant when $P \leq 1 - (1 - \alpha)^{1/k}$, where α is the experimentwise error rate and k is the number of tests (Sokal and Rohlf 1995:241). The second smallest P value was considered significant when $P \leq 1 - (1 - \alpha)^{1/k-1}$, and so on. Uncorrected P values are reported in the text and significant results after Dunn-Sidák correction are indicated with asterisks.

RESULTS

Relative abundance.—During the 1997 and 1998 field seasons combined, we detected 150 Red-eyed Vireos (74 and 76, respectively) and 74 Blue-headed Vireos (38 and 36, respectively) during the preplayback period. Thus, Red-eyed Vireos outnumbered Blue-headed Vireos approximately 2:1 on our study area.

Response to conspecific song.—Red-eyed Vireos responded to playback of conspecific song 45% (15/33) of the time, whereas Blue-headed Vireos responded 29% (8/28) of the time during 1997. During 1998, Red-eyed Vireos responded 61% (19/31) of the time and Blue-headed Vireos responded 29% (8/28) of the time. Red-eyed and Blue-headed vireos did not differ significantly between years in their likelihood to respond to conspecific song (Red-eyed Vireo: $G = 1.62$, df = 1, $P = 0.20$; Blue-headed Vireo: $G = 0.00$, df = 1, $P = 1.00$). The relative response of the two species to playback of their own song did not differ significantly from their relative abundance on

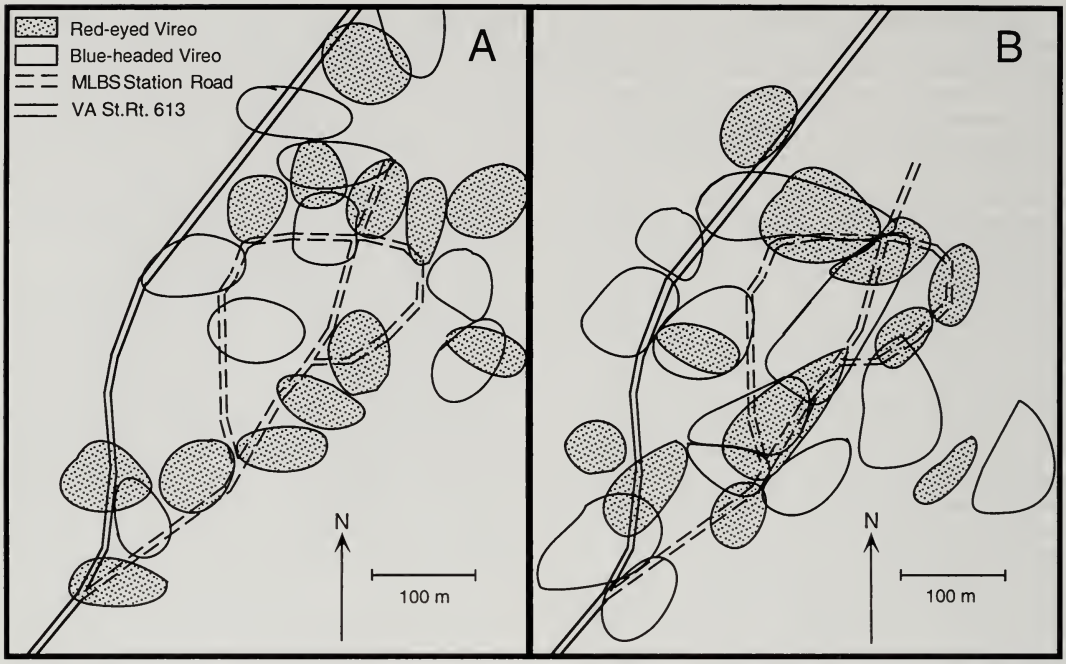

FIG. 1. Territorial overlap by Red-eyed (*Vireo olivaceus*) and Blue-headed (*V. solitarius*) vireos at Mountain Lake Biological Station, southwestern Virginia, during (A) 1997 and (B) 1998. Territories were determined using the recommendations of Bibby et al. 1993.

the study site as indicated by preplayback counts (1997: $G = 0.006$, df = 1, $P = 0.94$; 1998: $G = 0.06$, df = 1, $P = 0.80$).

Response to heterospecific song.—Red-eyed Vireos responded to heterospecific song 11% (3/28) of the time whereas Blue-headed Vireos responded 0% (0/33) of the time during 1997. During 1998, Red-eyed Vireos responded 7% (2/28) and Blue-headed Vireos responded 3% (1/31) of the time. The response of each species to heterospecific song was consistent with their relative abundance in the habitat (1997: $G = 2.4$, df = 1, $P = 0.12$; 1998: $G = 1.5$, df = 1, $P = 0.21$).

Territory overlap.—Territories of Red-eyed and Blue-headed vireos overlapped at MLBS during 1997 and 1998. During 1997, 5 of 13 (38%) Red-eyed Vireo territories overlapped Blue-headed Vireo territories, and 5 of 9 (56%) Blue-headed Vireo territories overlapped Red-eyed Vireo territories (Fig. 1A). Territorial overlap increased during 1998; 7 of 12 (58%) Red-eyed Vireo territories overlapped with Blue-headed Vireo territories, and 7 of 11 (64%) Blue-headed Vireo territories overlapped Red-eyed Vireo territories (Fig. 1B).

Habitat characteristics.—Although Blue-headed Vireos selected territories with a higher density of trees, Red-eyed and Blue-headed vireos occupied structurally similar habitats, whether structural variables were considered

TABLE 1. Structure characteristics of Red-eyed (*Vireo olivaceus*) and Blue-headed (*V. solitarius*) vireo habitats at Mountain Lake Biological Station, southwestern Virginia, 1997–1998. Values are means ± SE. Only the number of trees per plot differed significantly.

Species (plots)	Basal area (cm^2)	Trees per plot*	Shrubs per plot	Percent canopy cover
Red-eyed Vireo (43)	12,427 ± 471	24 ± 1	14 ± 2	72 ± 2
Blue-headed Vireo (32)	12,884 ± 621	28 ± 2	16 ± 1	71 ± 2

* $t = 2.19$, df = 73, $P = 0.032$.

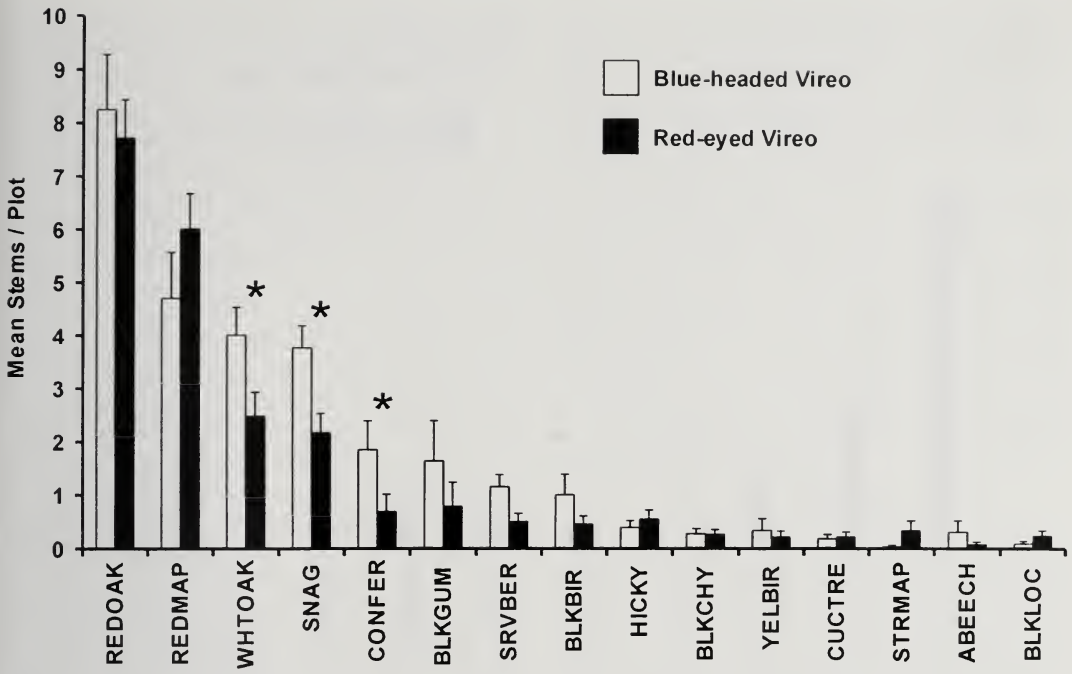

FIG. 2. Mean number of tree stems in Red-eyed (*Vireo olivaceus*, $n = 43$) and Blue-headed (*V. solitarius*, $n = 32$) vireo habitat plots at Mountain Lake Biological Station, southwestern Virginia, 1997–1998. Line above bar is 1 SE. Asterisks indicate significant differences between Red-eyed and Blue-headed vireo plots (WHTOAK and SNAG: *t*-test, adjusted $P < 0.05$; CONFER: Wilcoxon two-sample test, adjusted $P < 0.05$). Abbreviations for tree species classes and adjustment for P values are described in the text.

singularly (Table 1) or in a multivariate analysis of variance (MANOVA, Wilks' Lambda = 0.94, $P = 0.43$). Although structurally similar, univariate analysis characterized Blue-headed Vireo habitat as having significantly greater numbers of white oaks, conifers, and snags (Fig. 2). MANOVA indicated significant overall differences in tree species composition between vireo habitats (Wilks' Lambda = 0.703, $P = 0.047$) and canonical discriminant analysis showed that Red-eyed and Blue-headed vireo habitat is best discriminated based on the presence of striped maple and black locust (more common in Red-eyed Vireo habitat) and conifers and black birch (more common in Blue-headed Vireo habitat; Fig. 2). Red-eyed and Blue-headed vireo habitats did not differ significantly in shrub species composition, as indicated by univariate (Fig. 3) and multivariate analyses (MANOVA, Wilks' Lambda = 0.81, $P = 0.68$).

DISCUSSION

There is growing evidence that interspecific behavioral interactions within assemblages of vireos are geographically variable. For example, Red-eyed Vireos respond to sympatric congeners with (Rice 1978a, 1978b, 1978c) or without (James 1976, Robinson 1981) interspecific territoriality, depending on the species and location. Even in the absence of interspecific territoriality, Red-eyed Vireos may (Barlow et al. 1970, Robinson 1981) or may not (James 1976) show interspecific aggression. Our results from the southern Appalachians are consistent with the latter situation. Red-eyed and Blue-headed vireos lacked interspecific territoriality at Mountain Lake and showed low levels of interspecific aggression, as measured by response to heterospecific song. Greater response to song playbacks by Red-eyed Vireos was consistent with their greater relative abundance at Mountain Lake.

Given the lack of interspecific territoriality and aggression, previous studies of vireo assemblages suggest that Red-eyed and Blue-headed vireos at Mountain Lake should exhibit some other pattern of spatial segregation (James 1976). Red-eyed Vireos generally in-

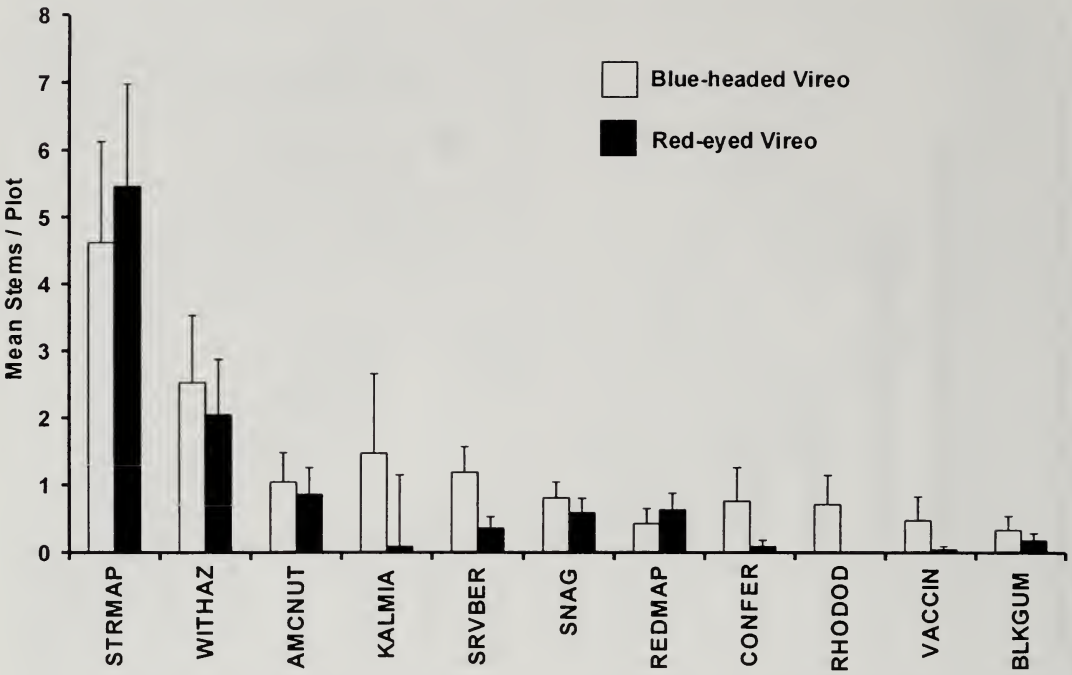

FIG. 3. Mean number of shrub stems in Red-eyed (*Vireo olivaceus*, $n = 43$) and Blue-headed (*V. solitarius*, $n = 32$) vireo habitat plots at Mountain Lake Biological Station, southwestern Virginia, 1997–1998. Line above bar is 1 SE. There were no significant differences between Red-eyed and Blue-headed vireo plots. Abbreviations for shrub species classes are defined in the text.

habit mature deciduous forests (Bent 1950, Hamilton 1962, James 1971) with some shrubs in the understory (James 1971), whereas Blue-headed Vireos generally inhabit coniferous or mixed deciduous-coniferous forests with sparse understory shrubs (Bent 1950, Hamilton 1962, James 1998). These generalizations lead to an expectation that Red-eyed and Blue-headed vireos at Mountain Lake might occupy slightly different microhabitats within their overlapping territories.

This was not the case regarding habitat structure. Based on the locations of singing or foraging individuals, Red-eyed and Blue-headed vireos occupied sites with similar tree size, density, and canopy cover. Nevertheless, there were slight but detectable differences in the tree species composition of the sites where we observed the two species. We observed Blue-headed Vireos in areas with significantly more white oaks, conifers, and snags, whereas we found Red-eyed Vireos in habitats with a relatively high abundance of red oaks and red maple (Fig. 2). Interestingly, species segregation (based on canonical discriminant analysis) was strongest for tree species that formed a relatively minor component of the forest at Mountain Lake. The tendency of Blue-headed Vireos to occupy sites with more conifers at Mountain Lake is consistent with qualitative reports of Blue-headed Vireo habitat preference (Bent 1950, Hamilton 1962, James 1998).

The habitat differences we observed in vireos at Mountain Lake were subtle, as were those documented by Sherry (1979) and Sherry and Holmes (1988) for American Redstarts (*Setophaga ruticilla*) and Least Flycatchers (*Empidonax minimus*) in New Hampshire. However, interspecific aggression appears to play a smaller role in reinforcing habitat segregation in Red-eyed and Blue-headed vireos than it did for redstarts and flycatchers (Sherry 1979, Sherry and Holmes 1988).

Although spatial (horizontal) segregation at the scale of the territory was not apparent and minimal in terms of microhabitat use, it remains possible that Red-eyed and Blue-headed vireos coexist by segregating vertically within the habitat by using different foraging

zones or nest sites. However, we detected only minimal differences in foraging height (SPH and CRC unpubl. data) at Mountain Lake. Furthermore, Red-eyed and Blue-headed vireos apparently built nests at similar heights at our study site (SPH and CRC unpubl. data). Published observations from other areas of sympatry also have failed to reveal pronounced vertical segregation (Cimprich et al. 2000, James 1998).

Based on the results of this and other studies (Bent 1950; Hamilton 1962; James 1971, 1998), preliminary foraging data, and behavioral characteristics such as nest site selection, apparent ecological segregation between Red-eyed and Blue-headed vireos was minimal at our study site and atypical of most sympatric vireo pairs (Hamilton 1962, Cody 1985). Red-eyed and Blue-headed vireos showed greater similarity in habitat use in the southern Appalachians than in the northern part of their ranges, but they did not increase interspecific aggression or diverge in foraging strategy (Petit et al. 1990; SPH and CRC unpubl. data). We believe the similarity in habitat use at our study site is a result of the relative availability of these species' preferred habitats. In other words, we suggest that Red-eyed and Blue-headed vireos respond to their own individualistic habitat cues (James 1971, Collins et al. 1982, Martin and Thibault 1996), but the nature of the habitat at Mountain Lake (conifers and birches broadly interspersed among dominant oaks and maples) precludes clear segregation by habitat. Additionally, ecological mechanisms other than territoriality and microhabitat segregation may be important in structuring the coexistence between these two species in the southern Appalachians.

Northern and southern subspecies of Blue-headed Vireo (*Vireo s. solitarius* and *V. s. alticola*, respectively) show slight morphological differentiation (generally larger in the south; James 1998), which may explain the qualitatively different foraging strategies employed by this species in the northern and southern Appalachians (Rabenold 1978, Robinson and Holmes 1982, Petit et al. 1990). Comparing the foraging strategies of Red-eyed and Blue-headed vireos in the southern Appalachians may further clarify the ecological factors potentially influencing their coexistence. Furthermore, a comparative analysis of habitat availability, habitat use, and foraging ecology between northern and southern populations of Red-eyed Vireos and both subspecies of Blue-headed Vireo may be necessary to tease apart subtle ecological differences between these two species.

We conclude that interspecific aggression and habitat association play only a small role in the ecological segregation of Red-eyed and Blue-headed vireos in the southern Appalachians. Furthermore, we suggest that quantitative analysis of basic patterns of ecological segregation can still yield important insights concerning local community structure and may be important in directing future forest management decisions.

ACKNOWLEDGMENTS

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RED-COCKADED WOODPECKER FORAGING BEHAVIOR IN RELATION TO MIDSTORY VEGETATION

D. CRAIG RUDOLPH,[1,2] RICHARD N. CONNER,[1] AND RICHARD R. SCHAEFER[1]

ABSTRACT.—Red-cockaded Woodpeckers (*Picoides borealis*) nest and forage in pine-dominated forests. Research indicates that substantial hardwood midstory encroachment is detrimental to Red-cockaded Woodpecker populations, although the exact mechanisms are unknown. We examined foraging behavior in relation to midstory between August 1989 and February 1990. Red-cockaded Woodpeckers foraged at greater heights in areas of taller and denser midstory in the loblolly-shortleaf pine (*Pinus taeda* and *P. echinata*, respectively) habitat, but not in longleaf pine (*P. palustris*) habitat with less-developed midstory vegetation than typical of loblolly-shortleaf pine habitat. In addition, Red-cockaded Woodpeckers concentrated foraging activities in or adjacent to forest stands or openings with reduced midstory vegetation. Overall, Red-cockaded Woodpeckers foraged disproportionately at heights and sites that minimized their exposure to dense midstory conditions. These results suggest that ecosystem management, preferably using prescribed fire, that reduces midstory vegetation will improve foraging habitat for Red-cockaded Woodpeckers. *Received 15 June 2001, accepted 12 February 2002.*

The Red-cockaded Woodpecker (*Picoides borealis*) is a federally listed endangered species endemic to fire-maintained pine forests of the southeastern United States (Jackson 1971, 1994). The Red-cockaded Woodpecker is a cooperatively breeding species, typically living in groups consisting of a breeding pair and one or more nonbreeding male helpers (Ligon 1970, Walters et al. 1988, Walters 1990). These groups occupy territories containing a cluster of one to several cavity trees and an adjacent foraging area (Hooper and Lennartz 1981, Hooper et al. 1982, DeLotelle et al. 1987, Walters 1990).

Populations of Red-cockaded Woodpeckers have declined drastically due primarily to loss of old growth pine habitat (Jackson 1971, Lennartz et al. 1983, Ligon et al. 1986, Conner and Rudolph 1989) and changes in the fire regime, resulting in increased midstory vegetation (Beckett 1971, Van Balen and Doerr 1978, Conner and Rudolph 1989). The species currently survives in small, typically isolated, and mostly declining populations in remaining areas of suitable habitat (James 1995).

The nearly complete elimination of wildfires due to efficient fire suppression measures and inadequate prescribed burning regimes have led to pervasive changes in the structure of the vegetation. Woody vegetation has greatly increased as the original fire-maintained pine-dominated communities enter the initial stages of succession to hardwood forest (Platt et al. 1988, Conner and Rudolph 1991, Frost 1993). Consequently, the open, pine-dominated stands with well-developed herbaceous understory vegetation that Red-cockaded Woodpeckers once inhabited are in most cases now pine-dominated stands with a well-developed hardwood midstory and greatly suppressed herbaceous understory (Platt et al. 1988, Conner and Rudolph 1991, Streng et al. 1993).

Numerous studies have noted that increasing midstory vegetation reduces the apparent suitability of habitat for Red-cockaded Woodpeckers (Van Balen and Doerr 1978, Repasky 1984, Hovis and Labisky 1985, Jackson et al. 1986). Midstory vegetation has been shown to increase the probability of cluster abandonment (Conner and Rudolph 1989), to negatively impact foraging (Epting et al. 1995), and to be negatively associated with measures of fitness (Davenport et al. 2000). How midstory vegetation leads to negative impacts on Red-cockaded Woodpecker populations is not well understood.

We examined the foraging behavior of Red-cockaded Woodpeckers to determine how Red-cockaded Woodpeckers react to different levels of midstory vegetation in predominately longleaf pine (*Pinus palustris*) forests and in mixed loblolly-shortleaf pine (*P. taeda* and *P. echinata*, respectively) forests in eastern Texas.

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STUDY AREAS AND METHODS

We examined Red-cockaded Woodpecker foraging behavior on the Angelina (31° 15′ N, 94° 15′ W) and Davy Crockett (31° 21′ N, 95° 07′ W) national forests in eastern Texas. Red-cockaded Woodpecker habitat on the Davy Crockett National Forest and the northern portion of the Angelina National Forest is composed primarily of loblolly and shortleaf pine with a significant hardwood component, especially in the midstory. Habitat on the southern portion of the Angelina National Forest is composed predominately of longleaf pine with a minimal hardwood component. Silvicultural practices near the study sites have included a mix of clearcutting, and seed tree or shelterwood harvests in which some mature trees are left unharvested. See Conner and Rudolph (1989) for a more complete description of the study sites.

Red-cockaded Woodpecker habitat is managed on both national forests to reduce midstory vegetation that has increased due to fire suppression (Conner and Rudolph 1989, 1991). Cluster sites have been a higher management priority than the surrounding foraging habitat. The primary result has been a major reduction in midstory vegetation within woodpecker cluster areas by a combination of prescribed fire, herbicides, and mechanical means. Midstory reduction in the foraging habitat surrounding the clusters, primarily using prescribed fire, has been much less effective, especially in the less pyrogenic loblolly-shortleaf pine habitat.

We banded members of 12 Red-cockaded Woodpeckers groups (6 in loblolly-shortleaf pine habitat, 6 in longleaf pine habitat) with metal USGS-BRD bands and plastic color bands for individual recognition. We determined social status of individuals (breeding pair, helpers, juveniles) by observing birds during the course of this study, especially during nesting. We used binoculars or a 20× spotting scope to identify birds and observe foraging behavior.

We observed foraging behavior of and habitat use by the 12 Red-cockaded Woodpecker groups between 29 August 1989 and 19 February 1990. This period was chosen to avoid influences of the nesting cycle on foraging patterns. Individual groups were observed for 1–5 days with a mean of 3.75 days. All groups included the breeding pair, and helpers and young of the year often were present as well. We initiated observations as group members exited roost cavities at dawn, and continued for approximately 3 h thereafter, for a total of 138 h on 45 different days. This time interval was chosen because it is typically a period of uninterrupted foraging. During the period of observation two observers, working as a team, attempted to maximize the number of woodpecker group members whose identity and foraging locations could be determined simultaneously. Simultaneous observations were necessary to allow collection of additional data for other aspects of this study. Once we located and identified a sufficient number of group members, we recorded foraging data. To maximize the likelihood that successive sampling observations would be independent, we maintained ≥10 min between sampling observations. This time interval was sufficient for individual birds to change foraging position in all cases, typically involving a change in foraging tree.

We measured the height above ground of individual birds using a clinometer. Trees in which the birds foraged were identified for subsequent relocation by recording unique characteristics and general location, supplemented by attaching plastic ribbon to the tree with identifying information.

Subsequently, we relocated foraging trees and obtained habitat measurements centered on the foraging tree. We recorded canopy and midstory basal areas of pine and hardwoods using a 1-factor metric prism. We also measured general canopy and midstory height, and foraging tree height using a clinometer, and estimated midstory density using a five-category scale, ranging from none (1) to very dense (5). We calculated standardized foraging heights as the percentage of tree height (foraging height/tree height × 100) for each foraging observation.

We selected a stratified random sample of trees to allow comparison of available trees with those used for foraging. Five pine trees were randomly selected per forest stand, a management unit delineated by the U.S. Forest Service, and habitat variables comparable to those for foraging trees were measured.

We also recorded the location of each foraging observation. Locations were characterized as (1) within intact forest (>50 m from an edge) or (2) open forest/edge, i.e., within or adjacent to (<50 m from) a forest opening, or within open forest. We defined forest openings to include clearcuts, pine plantations <20 years of age, road and utility rights-of-way, and other nonforested areas. We defined open forests to include seed tree and shelterwood harvest areas, southern pine beetle (*Dendroctonus frontalis*) infestation areas, and woodpecker cluster areas that had received some type of midstory control. We determined the percentage of area ≤800 m of the nest tree for each group of woodpeckers (an estimate of the group's foraging area) that occurred in each of these categories using forest stand maps and aerial photographs.

We compared habitat variables using *t*-tests. Satterthwaite's correction was used in cases of unequal variance. To avoid pseudoreplication, all data pertaining to individual birds and individual forest stands were treated as a single sample and analyzed accordingly. Bonferroni's correction was used to account for repeated testing of the same data set.

RESULTS

Comparisons of habitat variables measured at random trees in the two forest habitats (Table 1) revealed that loblolly-shortleaf pine habitats were characterized by significantly greater canopy height, midstory density composed predominately of hardwoods, and midstory hardwood basal area. We did not detect a significant difference in midstory height,

TABLE 1. Means (SD) of habitat variables for randomly selected canopy trees in longleaf pine habitat (n = 53 sites) and loblolly-shortleaf pine habitat (n = 44 sites), eastern Texas, 1989.

Habitat variable	Longleaf pine	Loblolly-shortleaf pine	P[a]
Canopy pine basal area[b]	16.8 (5.52)	15.4 (3.18)	0.1211
Midstory pine basal area	2.5 (1.88)	2.8 (2.22)	0.5412
Canopy hardwood basal area	0.3 (0.80)	0.8 (2.05)	0.1328
Midstory hardwood basal area	1.1 (1.87)	4.8 (2.97)	<0.0001
Canopy height[c]	22.2 (3.77)	27.1 (2.78)	<0.0001
Midstory height	8.3 (5.12)	10.7 (4.60)	0.0178
Midstory density	2.4 (0.97)	3.6 (1.32)	<0.0001

[a] Critical value of t-test with Bonferroni's correction is 0.0167.
[b] Basal area measures in m^2/ha.
[c] Height measures in m.

overstory pine basal area, midstory pine basal area, or hardwood overstory basal area between the forest habitats.

We obtained 944 foraging observations and corresponding habitat measurements for 41 individual Red-cockaded Woodpeckers from 12 groups, 510 in longleaf pine habitat and 434 in loblolly-shortleaf pine habitat. In longleaf pine habitat, the foraging sites used by Red-cockaded Woodpeckers had significantly greater canopy height compared to that measured at random trees (Table 2). Conversely, random sites had greater canopy pine basal area. In loblolly-shortleaf pine habitat, foraging sites had significantly lower canopy pine basal area and midstory density.

Red-cockaded Woodpecker foraging sites in longleaf pine habitats, compared to loblolly-shortleaf pine habitats, had significantly lower values for midstory hardwood basal area, canopy height, and midstory density (Table 3). Mean Red-cockaded Woodpecker foraging height was significantly greater in loblolly-shortleaf pine habitat (19.6 m) than in longleaf pine habitat (17.1 m). The corresponding standardized foraging height also was greater in loblolly-shortleaf pine habitat (72.5%) than in longleaf pine habitat (69.4%), although this difference was not significant.

In both longleaf and loblolly-shortleaf pine habitats, foraging height was positively correlated with canopy height (Table 4). In long-

TABLE 2. Means (ranges) of habitat variables for Red-cockaded Woodpecker (*Picoides borealis*) foraging trees and random trees in eastern Texas, 1989.

Habitat variable	Foraging trees	Random trees	P[a]
Longleaf pine habitat	n = 18	n = 53	
Canopy pine basal area[b]	14.2 (3.00)	16.8 (5.52)	0.0148
Midstory pine basal area	2.8 (1.67)	2.5 (1.87)	0.5292
Canopy hardwood basal area	0.3 (0.30)	0.3 (0.80)	0.9753
Midstory hardwood basal area	0.8 (0.82)	1.1 (1.87)	0.4062
Canopy height[c]	24.6 (1.23)	22.2 (3.77)	<0.0001
Midstory height	8.4 (2.28)	8.3 (5.11)	0.8625
Midstory density	2.2 (0.38)	2.4 (0.97)	0.4077
Loblolly-shortleaf pine habitat	n = 23	n = 44	
Canopy pine basal area	12.2 (2.52)	15.4 (3.18)	<0.0001
Midstory pine basal area	2.3 (1.60)	2.8 (2.22)	0.4202
Canopy hardwood basal area	0.4 (0.37)	0.8 (2.05)	0.1787
Midstory hardwood basal area	4.1 (1.72)	4.8 (2.97)	0.2326
Canopy height	26.8 (1.82)	27.1 (2.78)	0.5594
Midstory height	8.2 (3.41)	10.7 (4.60)	0.0288
Midstory density	3.0 (0.70)	3.6 (1.32)	0.0148

[a] Critical value of t-test with Bonferroni's correction is 0.0167.
[b] Basal area measures in m^2/ha.
[c] Height measures in m.

TABLE 3. Means (ranges) of habitat variables and foraging heights for Red-cockaded Woodpecker (*Picoides borealis*) foraging sites in longleaf pine habitat (n = 18 sites) and loblolly-shortleaf pine habitat (n = 23 sites), eastern Texas, 1989.

Habitat variable	Longleaf pine	Loblolly-shortleaf pine	P[a]
Canopy pine basal area[b]	14.2 (3.00)	12.2 (2.52)	0.0253
Midstory pine basal area	2.8 (1.67)	2.3 (1.60)	0.3744
Canopy hardwood basal area	0.3 (0.30)	0.4 (0.37)	0.5128
Midstory hardwood basal area	0.8 (0.82)	4.1 (1.72)	<0.0001
Canopy height[c]	24.6 (1.23)	26.8 (1.82)	<0.0001
Midstory height	8.4 (2.28)	8.2 (3.41)	0.8395
Midstory density	2.2 (0.38)	3.0 (0.70)	<0.0001
Woodpecker foraging height	17.1 (2.10)	19.6 (3.53)	0.0073
Standardized foraging height (%)	69.4 (8.53)	72.5 (10.17)	0.3039

[a] Critical value of t-test with Bonferroni's correction is 0.0167.
[b] Basal area measures in m^2/ha.
[c] Height measures in m.

leaf pine habitat, foraging height was negatively correlated with midstory pine basal area and canopy hardwood basal area. In loblolly-shortleaf pine habitat, foraging height increased as canopy pine basal area, midstory height, and midstory density increased.

Red-cockaded Woodpecker foraging trees were not randomly located; Red-cockaded Woodpeckers used trees within or adjacent to forest openings, or within cluster areas where midstory removal had occurred (open forest/edge areas), significantly more than expected. In longleaf pine habitat, 38.8% of foraging locations were in open forest/edge areas compared to an occurrence rate of 16.6% of this habitat (χ^2 = 84.7, df = 1, $P < 0.001$). In loblolly-shortleaf pine habitat, 67.8% of the foraging locations occurred in open forest/edge areas compared to an availability rate of 24.7% (χ^2 = 205.0, df = 1, $P < 0.001$). Openings with no foraging substrate (i.e., clearcuts and young plantations) were not included in these area calculations. Because data collection was limited to the first 3 h of each day, the possibility exists that there was a bias toward foraging within the stand containing the

TABLE 4. Correlation coefficients of Red-cockaded Woodpecker (*Picoides borealis*) foraging heights in relation to habitat variables in longleaf pine and loblolly-shortleaf pine habitats, eastern Texas, 1989.

Habitat variable	r	P
Longleaf pine habitat		
Canopy pine basal area[a]	0.250	0.574
Midstory pine basal area	−0.103	0.020
Canopy hardwood basal area	−0.092	0.038
Midstory hardwood basal area	−0.022	0.624
Canopy height[b]	0.397	<0.001
Midstory height	0.023	0.510
Midstory density	−0.031	0.493
Loblolly-Shortleaf pine habitat		
Canopy pine basal area	0.018	<0.001
Midstory pine basal area	0.009	0.856
Canopy hardwood basal area	0.060	0.219
Midstory hardwood basal area	0.035	0.469
Canopy height	0.513	<0.001
Midstory height	0.133	0.006
Midstory density	0.113	0.020

[a] Basal area measures in m^2/ha.
[b] Height measures in m.

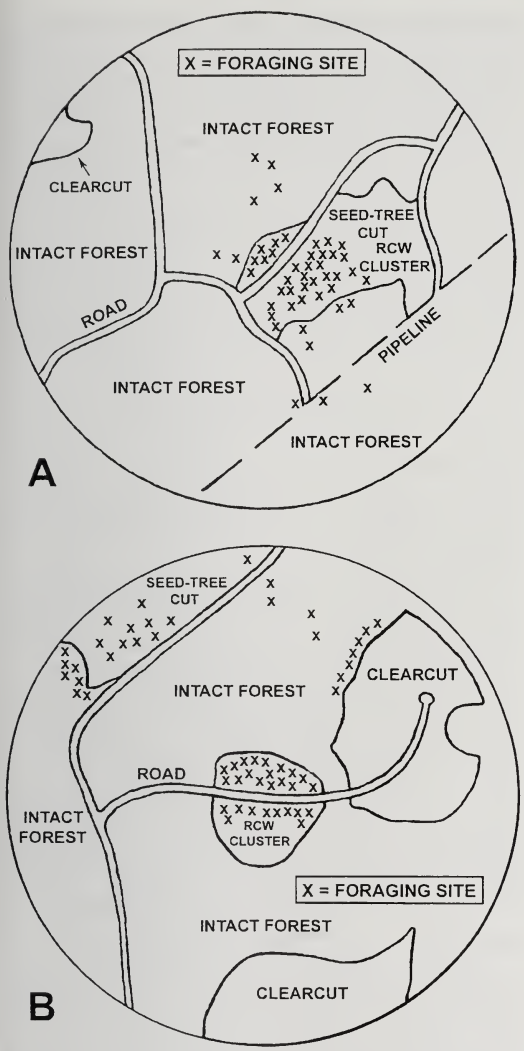

FIG. 1. Approximate locations of foraging sites of Red-cockaded Woodpeckers (*Picoides borealis*) on the Angelina National Forest in Texas, 1989. Examples from longleaf pine habitat (A) and loblolly-shortleaf pine habitat (B). Map circles are 800 m in radius centered on the woodpecker nest tree.

cavity tree cluster (see discussion). Removal of cavity tree cluster stands from the analysis eliminated the significant relationship in longleaf pine habitat ($\chi^2 = 7.73$, df = 1, $P = 0.26$), but not in loblolly/shortleaf pine habitat ($\chi^2 = 154.1$, df = 1, $P < 0.001$).

Foraging sites of two groups of woodpeckers illustrate habitat use by woodpecker groups in each pine habitat type (Fig. 1). The Red-cockaded Woodpecker group in the longleaf pine habitat concentrated their foraging in and adjacent to the seed tree harvest area containing the cavity tree cluster. Data from this group primarily were responsible for the different outcome with and without inclusion of the cavity tree cluster stand in the previous analysis. Surrounding intact interior forest habitat was closed canopy forest dominated by longleaf pine with moderate midstory development. The group of woodpeckers selected to illustrate habitat use in the loblolly-shortleaf pine habitat concentrated their foraging activities in and adjacent to a seed tree harvest area and adjacent to a recently planted clearcut, in addition to the cluster area where midstory removal had taken place.

DISCUSSION

Potential bias exists due to initiating observations in the cluster stands and the bird's periodic return to those stands. This potential bias was especially noticeable in the longleaf pine habitat due to timber harvest practices. The most open forest habitat available to several of the groups was the cluster area where the canopy had been thinned and midstory removed. In these instances the birds spent most of their foraging time in the cluster stand, unlike birds with additional open forest options available. Because birds with more options available frequently left the cluster area soon after exiting their roosts, and often returned later in the observation period, we believe that including the cluster area observations results in less bias than would result from deleting them.

The overall foraging behavior of Red-cockaded Woodpeckers in loblolly- shortleaf pine habitat indicated selection of foraging sites resulting in the avoidance of the typically dense midstory vegetation composed primarily of hardwoods. Red-cockaded Woodpeckers foraged in trees where the immediately adjacent habitat was characterized by significantly less dense midstory than what was available forestwide. In addition, Red-cockaded Woodpeckers foraged at greater heights at sites with greater midstory heights and densities.

These significant relationships were not detected in longleaf pine habitat. This may have been due to the significantly lower midstory density in the longleaf pine habitat than in the loblolly-shortleaf pine habitat. Midstory den-

sity at random points in longleaf pine habitat was less than midstory density adjacent to foraging trees in loblolly-shortleaf pine habitat.

Red-cockaded Woodpecker foraging height was positively correlated with canopy height in both habitat types, reflecting the increased range of potential foraging sites available in taller forest stands. In loblolly-shortleaf pine habitat, foraging height increased with canopy pine basal area, possibly due to a correlations among tree age, canopy height, and canopy pine basal area. In contrast, woodpecker foraging height was less in areas of longleaf pine habitat as midstory pine and canopy hardwood basal area increased. The relationship with midstory pine in longleaf pine habitat was the result of substantial amounts of woodpecker foraging directly on midstory pines in areas of relatively sparse midstory development, a behavior rarely noted in the loblolly-shortleaf pine habitat where midstory pines rarely occurred in areas of sparse midstory development. Many of the lower foraging heights observed in longleaf pine habitat with increased canopy hardwood basal area likely were due to substantial foraging in hardwood baygall habitats, which had lower canopy heights. The absence of a significant correlation between woodpecker foraging height and both midstory density and midstory height suggests that, in the longleaf pine habitats that we studied, midstory vegetation was not sufficiently developed to affect these aspects of woodpecker foraging behavior.

Canopy heights, both at foraging and random points, were significantly greater in loblolly-shortleaf pine habitat than in longleaf pine habitat. This difference was reflected in the overall significantly greater foraging height of Red-cockaded Woodpeckers in loblolly-shortleaf pine habitat.

In both habitat types, the distribution of foraging locations of Red-cockaded Woodpeckers suggests that midstory vegetation is a factor in foraging site selection across the landscape as well as within the vertical forest structure. In loblolly-shortleaf pine habitat, Red-cockaded Woodpeckers foraged disproportionately in forest stands that had reduced midstory vegetation, including cluster areas managed to reduce midstory vegetation and a variety of harvested areas where midstory as well as canopy vegetation had been reduced. Foraging frequently occurred adjacent to forest openings or stands with reduced midstory. Although midstory vegetation at the location of foraging might be substantial, midstory conditions adjacent to the foraging location generally were much reduced. In longleaf pine habitat, this pattern typically did not occur, presumably due to reduced levels of midstory vegetation throughout the landscape. Only in the one Red-cockaded Woodpecker group with access to a large seed tree cut, including the cavity tree cluster, did a pattern similar to what was observed in loblolly-shortleaf pine habitat occur. We suggest that these foraging patterns indicate an avoidance of contiguous habitat with dense and tall midstory vegetation. In eastern Texas this vegetation structure occurs primarily in loblolly-shortleaf pine habitat.

Historically, the primary management emphasis has been on the effects of midstory vegetation within cavity tree clusters. A number of hypotheses have been suggested to account for the observed impacts of midstory vegetation on Red-cockaded Woodpeckers: (1) increased vulnerability of the cavity to predators (Dennis 1971), (2) increased competition for cavities with other species (Loeb and Stevens 1995), and (3) an open flight path increasing ease of access to cavities (Wood 1983). However, direct evidence in support of any of these hypotheses is lacking.

Recent studies have detected potentially negative effects of midstory in the foraging area (Epting et al. 1995, Davenport et al. 2000). Our observations support the view that midstory vegetation results in foraging patterns that reduce use of habitats, or portions of habitats, where hardwood midstory vegetation is well developed. The adaptive significance of this behavioral pattern remains to be demonstrated. Recent studies indicate that prey availability is higher in habitats with less midstory vegetation and more herbaceous vegetation (James et al. 1997, Collins 1998), and woodpecker group reproductive fitness declines as midstory development in foraging habitats increases (Davenport et al. 2000). Thus, it is likely that there are direct effects of midstory vegetation on foraging. The data presented above demonstrate that Red-cockaded Woodpeckers forage less in habitat with well-developed hardwood midstory vegeta-

tion. This behavior is consistent with the results indicating lower prey availability and lower reproductive fitness as a response to increasing midstory vegetation due to changes in the fire regime of southeastern U.S. pine forests.

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DETERMINANTS OF DIETARY PREFERENCE IN YELLOW-RUMPED WARBLERS

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ABSTRACT.—Warblers are selective in what they eat, yet little is known about the dietary cues used by warblers as they decide what to eat. Semisynthetic diets may be useful for investigating how specific dietary cues, such as appearance or nutrient composition of food, influences diet preference of warblers because these dietary cues can be easily and systematically modified with semisynthetic diets. We offered Yellow-rumped Warblers (*Dendroica coronata*) paired choices of live waxworms (*Galleria mellonella*) and a waxworm mash, or waxworm mash and a semisynthetic mash. Birds strongly preferred live waxworms over waxworm mash, suggesting that natural appearance of food strongly influences diet preference of warblers when the nutrient composition of diets is similar. When birds initially were offered the two mash diets, they consistently preferred waxworm mash over semisynthetic mash within the first 15 min with food, suggesting that they were using dietary cues that provided rapid feedback as would be provided by a cue such as taste. This initial preference for waxworm mash was maintained for the first two days, but then the warblers ate similar amounts of waxworm mash and semisynthetic mash during the last two days of the experiment. The decrease in preference for waxworm mash over time probably occurred because at least some of the cues used by the birds in determining their diet preference(s) required days for reliable feedback. Thus, diet preferences of warblers apparently were influenced by dietary cues that provided immediate and delayed, postingestional feedback. These results support the use of semisynthetic diets in studies of avian diet preferences and highlight the importance of adequate acclimation time on test diets. *Received 19 June 2001, accepted 11 March 2002.*

Descriptive studies of the diet and foraging behavior of warblers (family Parulidae) have provided the foundation for testing important ecological theory related to niche partitioning (MacArthur 1958; Morse 1980, 1989), competition (Wiens 1989), and optimal foraging (Zach and Falls 1976, 1978). Most such descriptive studies have compared food use and availability, and have demonstrated that warblers are selective in what they eat (Morse 1989). However, predicting the diet of warblers also requires an understanding of their diet preferences which can be investigated by allowing an animal equal access to certain food types and measuring relative use (Johnson 1980, Litvaitis et al. 1996). Diet preference likely is related to the nutritional adequacy of foods whereas diet selection is a function of the interaction between diet preference and the availability of alternative foods. Thus, an understanding of the dietary cues used by warblers as they decide what to eat is necessary for accurately predicting both diet preferences and diet selection of warblers.

Free-living warblers and other passerine birds may use a variety of dietary cues to decide what to eat, including sensory cues such as appearance, taste, smell, and texture of the food (Willson et al. 1990, Willson 1994) and the nutritional adequacy of the food itself (Murphy and King 1987, Cipollini and Levey 1997, Lepczyk et al. 2000). The relative importance of certain cues in determining diet preferences can be inferred from measurements of temporal changes in diet choice since dietary cues differ in how rapidly they can be detected. For example, dietary cues such as color are immediately apparent to birds whereas postingestive cues related to the nutritional adequacy of the diets may take days for reliable feedback.

Since natural foods often differ markedly in nutrient composition and other dietary cues, we used semisynthetic diets to identify which dietary cues were important in determining diet preferences of Yellow-rumped Warblers (*Dendroica coronata*). Semisynthetic diets are useful in studies of avian diet preference and nutritional ecology because the exact nutrient composition of such diets is known, and because semisynthetic diets are easily and accurately replicated or manipulated (Murphy and King 1982). Although semisynthetic diets can be formulated to match the nutrient composition of the bird's natural diet, they often

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TABLE 1. Composition (per 100 g) of two mash diets and of whole waxworms[a] (*Galleria mellonella*). These three diets were used to determine how specific dietary cues such as appearance or nutrient composition of food influences diet preferences of Yellow-rumped Warblers (*Dendroica coronata*).

Experimental diet	Ingredients	Wet mass	Dry mass
Semi-synthetic mash	Carbohydrates (D-glucose)	1.13	10.04
	Protein (casein[b])	6.80	52.30
	Fat (olive oil)	2.61	20.08
	Vitamin mix[c]	0.22	1.67
	Salt mix[d]	0.76	5.86
	Agar	1.31	10.00
	Water	87.00	
Waxworm mash	Carbohydrates	0.70	6.92
	Protein	3.35	33.00
	Fat	4.42	43.63
	Calcium	0.01	0.03
	Ash	0.20	1.93
	Agar	1.47	14.49
	Water	89.85[e]	

[a] Composition of whole waxworms is the same as waxworm mash without agar and added water.
[b] Casein = (high N) Teklad, U.S. Biochemical Corp., Cleveland, Ohio.
[c] AIN-76 Vitamin Mix, ICN Biomedicals, Inc.
[d] Salt mix = ICN Biomedicals, Inc. (Spivey-Fox and Briggs 1960).
[e] 11.49% of water is from waxworms.

are quite different in appearance (e.g., mash diets used by Afik and Karasov 1995, Afik et al. 1995, McWilliams and Karasov 1998). In this study, we used live waxworms (*Galleria mellonella*), minced waxworms, and a semisynthetic mash diet to determine how visual appearance and nutrient composition of diets influenced the warbler's choice of diets.

METHODS

Study subjects and maintenance.—We used mist nets to capture 20 Yellow-rumped Warblers in southern Rhode Island during October 1998. Prior to the experiments, birds were maintained in the laboratory for 15 weeks and were fed a semisynthetic mash (Table 1) and live waxworms. This semisynthetic mash is similar to the nutrient composition of insects (10% carbohydrates, 52% protein, and 20% fat; Bairlein 1987) and has been used to maintain Yellow-rumped Warblers in the laboratory for months (Afik and Karasov 1995, McWilliams and Karasov 1998). Birds were weighed and given fresh food and water between 07:30 and 09:00 EST each day. Birds were housed individually in stainless steel cages (60 cm × 20 cm × 35 cm) in a room with 10L:14D light and 21° C temperature regimes.

During February 1999, we acclimated all 20 birds to the paired dish protocol and the three food types used in the preference tests (Table 1). Throughout the 3-day acclimation period and during both experiments, birds always were offered food in two dishes on opposite sides of the cage (about 10 cm apart). During the 3-day acclimation period, one dish contained 20 g of waxworm mash and three live waxworms and the other dish contained 20 g of semisynthetic mash and three live waxworms. Each day we switched the location of the food types to ensure food position did not bias the preference results (see Jackson et al. 1998). This acclimation period was designed to reduce any effect of previous short term experience on diet preference of warblers. However, if diet preference is determined primarily by the duration of time spent feeding on a diet over months rather than days, then warblers should prefer the semisynthetic mash and live waxworms (fed to these birds for 3 months) over waxworm mash (fed to these birds for 3 days).

Preference tests.—In experiment 1, we offered 15 g of waxworm mash in one dish and 20 live waxworms (about 15 g) in another dish to each of the 20 birds. We weighed each dish with 20 waxworms to determine total mass of waxworms offered. For experiment 2, we offered 20 birds 15 g of waxworm mash in one dish and 15 g of semisynthetic mash in another dish. In both experiments, the food was available from 08:00–12:00. After the 4-h test period, the food dishes were weighed and then replaced with two dishes each containing 10 g of semisynthetic mash. Subsamples of food were dried at 100°C to estimate dry matter intake. All birds had food remaining after the 4-h test period and by morning, so that the feeding regime each day was *ad libitum*.

In both experiments, we observed some birds during the first hour (08:00–09:00) with food to determine which food type was eaten first and visited most frequently. For experiment 1, we randomly selected 10 of the 20 birds for observation on day 1 and then we observed the same 10 birds on day 2. For experiment

TABLE 2. Captive Yellow-rumped Warblers (*Dendroica coronata*; $n = 20$) ate predominately live waxworms when offered a choice of live waxworms and minced waxworms (experiment 1), and eventually ate similar amounts of each diet when offered a choice of minced waxworms and a semisynthetic diet (experiment 2). Values for food intake are means ± SE.

	Food intake (g dry/4 h) of warblers given a choice of two diets					
	Live waxworms	Waxworm mash	Semisynthetic mash	Total food intake[a]	t[b]	P
Experiment 1						
Day 1	1.48 ± 0.09	0.08 ± 0.01		1.56 ± 0.07	20.95	<0.01
Day 2	1.45 ± 0.06	0.16 ± 0.01		1.56 ± 0.06	24.45	<0.01
Experiment 2						
Day 1		0.64 ± 0.04	0.30 ± 0.04	0.94 ± 0.04	4.42	<0.01
Day 2		0.78 ± 0.04	0.28 ± 0.06	1.06 ± 0.05	5.73	<0.01
Day 3		0.74 ± 0.06	0.78 ± 0.25	1.52 ± 0.09	−1.10	0.77
Day 4		0.52 ± 0.04	0.68 ± 0.47	1.20 ± 0.17	−0.30	0.28

[a] Total food intake was similar between days in experiment 1 ($P > 0.90$), whereas total food intake increased across days in experiment 2 ($F_{3,57} = 5.75$, $P = 0.002$).

[b] Two-tailed paired t-test with 19 df comparing food intake of live waxworms and waxworm mash in experiment 1 or waxworm mash and semisynthetic mash in experiment 2.

2, we observed all 20 birds on day 1 and again on day 3. We made observations from behind a blind that had been in the room for two weeks prior to the experiment.

Food preference was determined by comparing the amount of food that had been consumed during the 4-h test period, the number of birds that visited each food type first, and the mean frequency of visits to each food type during the first four 15-min periods with food each day.

Statistical analysis.—For both preference tests, we used a two-tailed paired t-test to determine if there was a significant difference between days in the amount of each food type eaten. In experiment 1, we also used a two-tailed paired t-test to determine if there was a significant difference between days in the proportion of food intake composed of live waxworms. We used a chi-square test to determine if more birds fed first on one food type than the other, assuming no preference. In experiment 1 and experiment 2, we used a repeated measures ANOVA to determine if the preferences of birds changed during the first hour with food. For experiment 1, the dependent variable was the proportion of food intake composed of live waxworms. For experiment 2, the dependent variable was the proportion of food intake composed of waxworm mash. In experiment 2, we used a repeated measures ANOVA to determine if the preferences or total food intake of birds changed across days. For all statistical tests, a P value <0.05 was considered significant. All results are presented as mean ± SE.

RESULTS

In experiment 1, birds ate significantly more live waxworms than waxworm mash on both day 1 (95.09% ± 0.01) and day 2 (92.66% ± 0.01; Table 2). This difference between days was statistically significant ($t_{19} = 2.27$, $P = 0.018$) because birds ate slightly more of the waxworm mash on day 2 (Table 2).

In experiment 2, total food intake during the 4-h test period increased across days as more semisynthetic mash was consumed on days 3 and 4 (Table 2). The proportion of food intake composed of waxworm mash declined significantly across days ($F_{3,57} = 6.94$, $P < 0.0001$). Birds ate significantly more waxworm mash than semisynthetic mash on day 1 (68.53% ± 0.04) and day 2 (75.63% ± 0.04), but showed no significant difference on day 3 (53.34% ± 0.05) or day 4 (53.62%; 0.05; Table 2). We calculated the statistical power to detect a 0.10 g difference in food intake assuming $\alpha = 0.05$ and using the estimated within-group variance from our experiment. The power in this case was 95.5%. Thus, there was a 95.5% probability of detecting a 0.10 g difference in food intake between the two mash diets at the 5% level of significance.

In experiment 1, all 10 birds that were observed during the first hour with food ate a live waxworm first on both day 1 and day 2. In experiment 2, similar numbers of birds ate first from the waxworm mash (12 birds) and semisynthetic mash (8 birds) on day 1 ($\chi^2 = 0.80$, df = 1, $P = 0.39$), whereas significantly more birds ate waxworm mash first (19 birds) on day 3 ($\chi^2 = 16.25$, df = 1, $P < 0.0001$).

In each of the four 15-min periods during the first hour with food, birds in experiment 1 visited the dish with live waxworms more often than the dish with waxworm mash (time effect: $F_{3,54} = 1.36$, $P = 0.26$; day effect: $F_{1,18} = 0.06$, $P = 0.81$; day × time effect: $F_{3,54} = 0.23$, $P = 0.87$). On both day 1 and day 2, birds visited the dish with live waxworms 86% ± 9.3 of the time during the first 30 min with food compared to 68% ± 14.9 of the time during the next 30 min. During the first 15-min period on day 1, birds in experiment 2 visited the dish with waxworm mash as often as the dish with semisynthetic mash. However, during the next three 15-min periods on day 1 and during all four 15-min periods on day 3, birds visited the dish with waxworm mash a mean of 81% ± 5.2 of total visits compared to the dish with semisynthetic mash (time effect: $F_{3,114} = 3.06$, $P = 0.031$; day effect: $F_{1,38} = 2.61$, $P = 0.11$; day × time effect: $F_{3,114} = 2.74$, $P = 0.046$).

DISCUSSION

Yellow-rumped Warblers consistently ate live waxworms first, they visited the dish with live waxworms more frequently during the first hour with food, and >90% of their diet during each 4-h test period was live waxworms. Given that live waxworms and waxworm mash have the same nutrient composition, the preference for live waxworms is likely due to the familiar appearance of the live caterpillars to the insectivorous warblers. Similarly, granivorous White-throated Sparrows (*Zonotrichia leucophrys*) preferred a semisynthetic mash shaped like seeds to the powdery form of the same diet (Murphy and King 1982). Thus, natural appearance of food influences diet preference of birds, especially when the nutrient composition of alternative diets is similar.

When Yellow-rumped Warblers initially were offered a choice between the two mash diets, they sampled both diets during the first 15 min with food and then settled on a consistent preference for waxworm mash over semisynthetic mash. Such short term sampling of diets at first offering was not evident when the birds were offered live waxworms and waxworm mash. Denslow et al. (1987) also found that birds required more sampling time when offered mash diets compared to natural diets. Apparently when two mash diets are offered, the warblers must base their preference on properties of the foods that are not detectable prior to ingestion so that sampling is necessary. Such sampling of foods with similar appearance also has been observed in bumblebees (*Bombus* spp.) choosing flowers (Oster and Heinrich 1976) and in mammalian herbivores (e.g., equines, ungulates, and lagomorphs) choosing rangeland plants (Westoby 1974, 1978). Given that the warblers' diet choice did not change after the first 15 min with food, the postingestive cues used by the warblers provided rapid feedback as would be provided by a cue such as taste.

Despite a consistent preference for waxworm mash over semisynthetic mash during the first hour with food, Yellow-rumped Warblers did not consistently eat more waxworm mash than semisynthetic mash during the entire 4 h with the diets on all four days of experiment 2. Warblers preferred waxworm mash during the first two days of experiment 2, but they ate similar amounts of waxworm mash and semisynthetic mash during the last two days of experiment 2. The change in preference across days occurred primarily because warblers increased their consumption of semisynthetic mash as well as total intake between the first two and the last two days of experiment 2. Such a temporal change in diet preference across days may occur (a) if birds must become familiar with the diets (Greenberg 1983, Murphy and King 1987, Avery et al. 1995), (b) if birds can not satisfy their nutrient requirements on only one of the diets (Murphy and Pearcy 1993), or (c) if the process of sampling and choosing diets involves cues that require days for reliable feedback.

The first two hypotheses are unlikely to explain the temporal change in diet preference across days that we observed. In general, Yellow-rumped Warblers eat a diversity of foods in the wild (Hunt and Flaspohler 1998) and so are unlikely to exhibit feeding neophobia as observed in some species of warblers and sparrows that are feeding specialists (Greenberg 1983, 1990). In addition, the design of our experiment included at least three days of acclimation on the experimental diets so that birds were familiar with those diets. Furthermore, the warblers used in this experiment have maintained body mass for weeks when

fed only semisynthetic mash (this study) or waxworm mash (SRM unpubl. data), both supplemented with several live waxworms. Thus, both diets apparently are nutritionally adequate, and both diets were familiar to these warblers prior to the experiments.

The similar appearance and consistency of the waxworm mash and semisynthetic mash apparently required warblers to extensively sample the diets offered and use cues that required days for reliable feedback. The birds initially may have preferred waxworm mash in experiment 2 because they had just completed experiment 1 in which they were offered live waxworms and waxworm mash. After two days of sampling both diets, however, warblers ate equivalent amounts of waxworm mash and semisynthetic mash, suggesting no preference. McPherson (1988) found that Cedar Waxwings (*Bombycilla cedrorum*) also changed their diet preference over time, from an initial preference for small, red, semisynthetic berries over large, nonred berries to no preference. Given that the warblers' and waxwings' diet choice changed only after two days, the postingestive cues used by these birds must have provided delayed feedback as would be provided by a cue such as maintenance of body mass or certain fat reserves.

Yellow-rumped Warblers always ate some of both diets offered, even when provided live insects that they strongly preferred. Such "partial preferences" (after Krebs and McCleery 1984) may occur because warblers are sampling to better assess their diet choices. During their sampling of the two mash diets, warblers used cues with both immediate and delayed feedback to determine their diet preferences as indicated by temporal changes in their diet choices.

If semisynthetic diets that appear different from natural foods are used to investigate the nutritional cues that determine diet preferences of birds (e.g., Murphy and King 1987, this study), then birds must be given adequate acclimation time so that the birds' preferences can be determined independent of the process of diet sampling. In the case of Yellow-rumped Warblers eating simple mash diets, an acclimation period of at least three days seems necessary. If color is added to the mash diets, then birds may use visual cues to determine diet type (Schuler 1983, Lepcyck 1993, Whelan and Willson 1994, Willson 1994) and this may reduce the time delay associated with using other cues that provide delayed feedback. In summary, these results support the use of semisynthetic diets in studies of avian diet preferences and highlight the importance of adequate acclimation time on test diets.

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DELAYED VOCAL MATURATION IN POLYGYNOUS YELLOW-RUMPED CACIQUES

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ABSTRACT.—Almost all songbird males develop fully crystallized songs before or during their first potential breeding season, when they use these important signals during interactions that determine their social success. We describe a rare phenomenon, in which vocal maturation is delayed until the second potential breeding season, or third year of life, in Yellow-rumped Caciques (*Cacicus cela vitellinus*) from lowland Panama. We heard predefinitive males in their second year sing only uncrystallized song, while three definitive males known to be in their third year sang fully developed songs matching the local dialect. The unusual system of polygynous breeding colonies in caciques may account for why vocal development is delayed. We would expect to find other examples of delayed vocal maturation in polygynous, nonterritorial species, in which second-year males have little opportunity for social success. *Received 25 July 2001, accepted 1 July 2002.*

Delayed vocal maturation, which we define as the failure of a songbird to develop crystallized song before or during the first potential breeding season, is a rare phenomenon not previously reported in the literature. Song acquisition in songbirds occurs in two phases: a memorization phase, in which acoustic information is stored in the brain after exposure to conspecific song, and a crystallization phase, during which songs are practiced and refined using auditory feedback to compare song output with signals stored in the neural pathways (Konishi 1965, Nottebohm 1999). Memorization of the first songs usually occurs within a few months of hatching, but in some species continues into the first breeding season (Kroodsma 1982, Nelson et al. 1995, Slater and Jones 1995, Waling et al. 1998, Nordby et al. 2001). Other birds continue to acquire new songs or to modify existing ones beyond the yearling period, which may result in increased repertoire size (Nottebohm and Nottebohm 1978, Mountjoy and Lemon 1995), adoption of new local dialect variants (Payne 1985, Trainer 1989), or refining an existing song (O'Loghlen and Rothstein 1993). Studies generally have revealed little variation in the timing of song crystallization. Nearly all songbird species develop their first fully crystallized songs shortly before or sometime during the initial breeding season after hatching (Kroodsma 1982). This timing ensures that males have vocal signals needed to attract mates, defend territories, or advertise social status. The existence of birds that pass the first breeding season without this important social signal requires explanation. Here we describe delayed vocal maturation in Yellow-rumped Caciques (*Cacicus cela vitellinus*) based on observations of color-banded birds in the field, and discuss reasons why it evolved in light of the unique natural history of this species.

Yellow-rumped Caciques build their hanging nests in tight clusters of 20–100 nests in colonies consisting of one or two trees. Males gather in the nest tree to sing, frequently supplanting one another, and occasionally chasing others out of the tree (Trainer 1988). Colony residents share dialects of 5–7 song types that differ from those at other colonies. Members of a colony exhibit a great deal of uniformity in their renditions of shared song types. The maintenance of this uniformity appears to have great social significance; despite rapid change in the structure of each song type throughout the breeding season, song uniformity persists because each member of a colony adopts the changes. Furthermore, when breeding males disperse between colonies from one breeding season to the next, they adopt the local song types and drop their previous repertoires (Trainer 1989). During bouts of countersinging, males match each other's song types, which probably helps maintain the linear dominance hierarchy (Trainer 1988).

Dominant males monopolize preferred singing sites nearest the nests, and are most successful at forming sequential consortships with 1–27 females. Males guard their consorts, following them between the nest tree

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TABLE 1. Hatching-year and second-year Yellow-rumped Cacique (*Cacicus cela vitellinus*) males had shorter wings[a] and lower body mass[b] than after-second-year males. Data are from Panama, January to May, 1981–1983.

	Wing chord			Body mass		
	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*
After-second-year males	174.87	4.30	23	120.84	6.72	19
Hatching-year and second-year males	155.06	7.39	17	111.65	8.25	17

[a] $t = 9.88$, $P < 0.005$.
[b] $t = 3.64$, $P < 0.005$.

and the surrounding forest, where females forage or gather nest material (Robinson 1986). Males do not contribute to nest building or rearing young in this system of female defense polygyny. Males acquire the definitive black and yellow plumage by their third year. Second-year (SY) males have a distinct plumage, with darker eyes and olive edges on the contour feathers (Jaramillo and Burke 1999).

METHODS

We conducted our study at one breeding colony in the lowland forest near the Pacific entrance to the Panama Canal (8° 54′ N, 79° 34′ W) from January to May, 1981–1983. We captured caciques in mist nets suspended from 10-m aluminum poles and banded them with colored PVC bands and a numbered, monel metal band. We recorded body weight, wing chord, and cloacal protuberance of each male captured, and aged individuals on the basis of plumage and eye color. Our analysis of vocal behavior of SY males is based on 360 h of observation of breeding activity at one colony from 16 February to 15 April 1983. We observed 32 occurrences of singing, each lasting 15–45 min, performed by 20 different SY males. SY males, hatched during the previous breeding season, January to May 1982, were 9–15 months old. Males of other songbird species generally have crystallized song by these ages. To compare the behavior of SY males with after-second-year (ASY) males, we noted supplanting, chasing, and grappling among males, and courtship and copulation with females. We recorded songs using a Marantz PMD 340 cassette recorder and an Uher M517 cardioid microphone, and made sonograms using a Kay Elemetrics Model 5500 Sound Spectrum Analyzer with a grey scale video printer.

RESULTS

We found no overlap in the sizes of predefinitive and definitive males; hatching-year and SY cacique males had significantly shorter wing chords and lower body weight than ASY males (Table 1). Furthermore, the first three outer primary feathers of SY males lacked the notched, tapered ends characteristic of definitive males. SY males failed to produce the noisy wing beats that ASY males sometimes produce just before landing in the nest tree as part of a flight display. Only 3 of 17 (18%) SY males captured had cloacal protuberances greater than 5 mm, whereas 22 of 23 (96%) of ASY males did.

In the nest tree, SY males generally sat quietly, moved around looking into nests, or chased females as they left the nest tree. When threatened by an ASY male, they adopted a subordinate posture with wings drooping and tail flared. During 78 encounters between SY and ASY males, the older birds always supplanted the younger birds. On a few occasions when an SY male began to vocalize in the nest tree, he was immediately chased from the tree by an ASY male. We did not see any copulations involving SY males, although sightings of matings by ASY males also were infrequent in the study area. Sometimes an SY male performed the precopulatory display toward another SY male, but never toward a female. This display is a seemingly robotic series of head-up poses alternating with tapping the yellow rump patch of the recipient.

Despite constant singing activity by ASY males during daily observation periods, we heard bouts of singing by SY males only 32 times. These bouts occurred only in the forest adjacent to the nest tree, and were either undirected or directed toward a female when she entered the forest. SY males sang only bouts of uncrystallized songs. These bouts differed from those of ASY males in that they were softer, contained numerous incomplete songs, contained unique renditions that occurred only once and did not match any of about 50 song types recorded within 8 km of the nest colony, contained songs that matched local song types but were variable in structure when repeated,

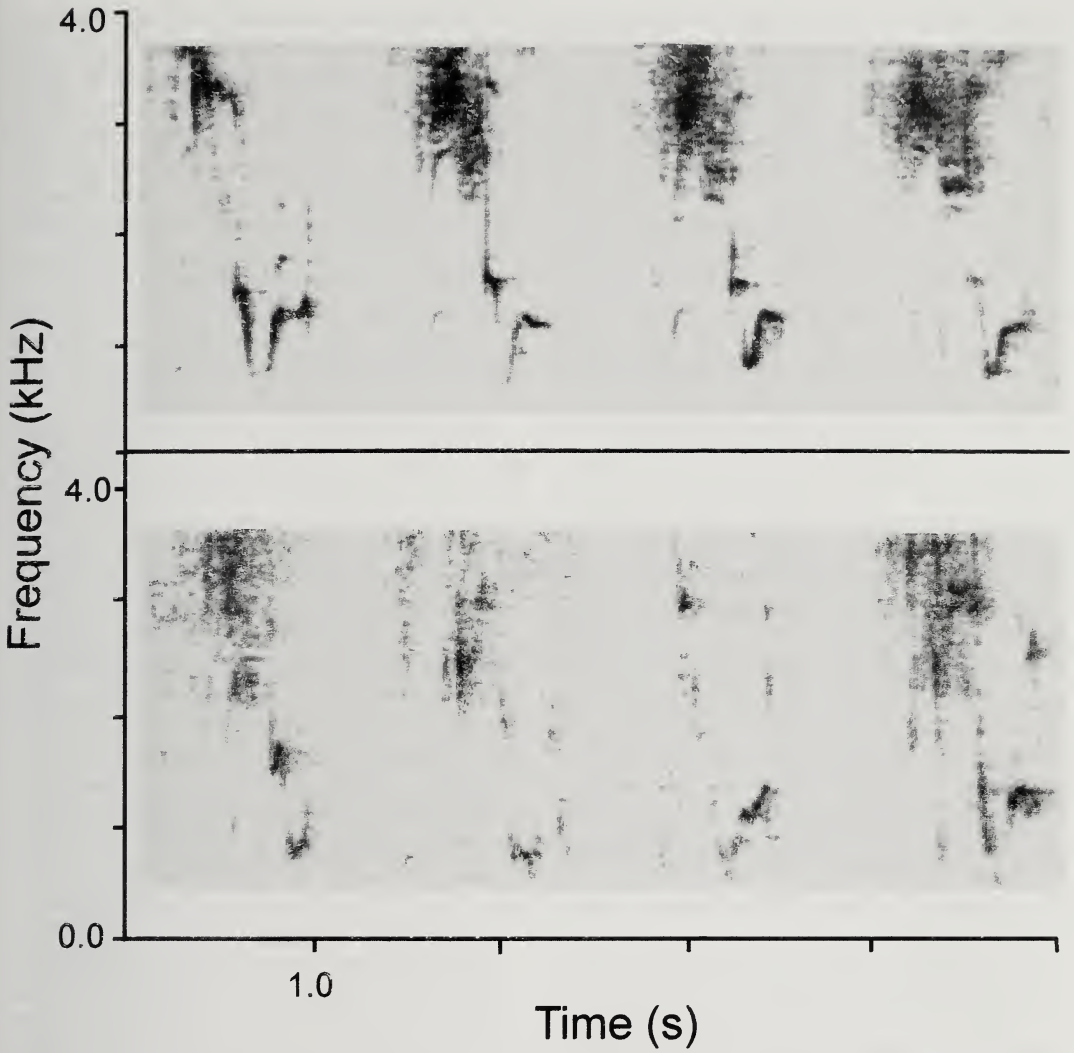

FIG. 1. (Top) The same crystallized song type sung by four Yellow-rumped Caciques in definitive plumage were stereotyped within males and differed little among males. (Bottom) The same song type varied among four uncrystallized renditions sung by one second-year male, and differed structurally from the songs of definitive males. All songs were recorded at the same colony in Panama on 17 April 1983 by J. M. Trainer. Sonograms were made with a Kay Elemetrics Model 5500 Sound Spectrum Analyzer.

and contained song types from more than one colony (Fig. 1). In contrast, ASY males sang only loud bouts in which they repeated stereotyped renditions of song types from only one colony. Three color-banded males, known to be third-year males because they were banded the previous year in predefinitive plumage, sang fully crystallized song.

DISCUSSION

These observations led us to conclude that fully crystallized song matching the local dialect appears by the third year in Yellow-rumped Cacique males when they are 21–27 months old. During their second year, or the first potential breeding season, they sing infrequently and then only uncrystallized songs. Hence, song maturation in caciques coincides with acquisition of the definitive plumage. Because we did not examine gonads or measure hormone levels of male caciques, we do not know the relationship between sexual maturity and vocal development. In some songbirds,

increasing steroid hormone levels during the first spring after hatching cause songs to crystallize (Marler et al. 1988, Whaling et al. 1998). Perhaps male caciques do not experience sufficient testosterone levels for song crystallization until their third year.

These findings contrast with numerous songbird species in which crystallized songs develop in time for the first potential breeding season. Even among dozens of species in which SY males have a predefinitive plumage, males are sexually mature, exhibiting normal courtship and singing behavior (Rohwer et al. 1980). Predefinitive SY males of both monogamous and polygynous species sometimes are successful at acquiring territories and mates (Rohwer et al. 1980, Payne 1982). As long as there is some chance of establishing a territory or attracting a mate, it may benefit males to develop crystallized song, even if they retain predefinitive plumage (Studd and Robertson 1985).

However, Yellow-rumped Caciques have an unusual natural history that may account for occurrence of delayed vocal maturation. We propose four factors that explain this rare phenomenon in caciques. First, SY males have almost no chance for reproductive or competitive success. Our observations in Panama and Robinson's (1986) observations of caciques in Peru indicate that the low dominance status of SY males prevents them from monopolizing singing perches, forming consortships or copulating. Because competitive interactions among males occur in breeding aggregations, reproductive interference may make it nearly impossible for young males to reproduce successfully. Selander (1972) similarly argued that delayed plumage maturation is favored by natural selection when young males have a reduced probability of reproductive success. Like caciques, many songbirds with predefinitive plumages are polygynous (Rohwer et al. 1980). The unlikelihood of breeding mitigates the cost of spending the second year with a less effective social signal, be it predefinitive plumage or uncrystallized song.

Second, failure to sing crystallized song in caciques may signal low social status, inviting less aggression and more tolerance from adult males. Similar hypotheses have been proposed for the advantage of having a dull, predefinitive plumage. Males in such plumages may resemble females or juveniles (Rohwer et al. 1980, Lawton and Lawton 1986), or signal low social status (Lyon and Montgomerie 1986), resulting in less aggression from older males. Unlike many plumage signals, however, song can be switched off in order to avoid an aggressive encounter. Young males with crystallized songs can avoid aggression simply by remaining silent in the presence of a dominant individual. The avoidance of aggression may help explain why SY cacique males avoid singing crystallized song, but additional factors are needed to explain why they fail to develop crystallized song.

Third, were males to develop crystallized songs during their second year, their songs would be socially inappropriate when they later began to breed. Unlike adults, SY males moved among colonies frequently during a breeding season, often appearing at several colonies during a period of a few days (Trainer 1989). Sixty-seven percent of SY males appeared in a different colony the following year when they began to compete for mates. Furthermore, 78% of song types at a colony were different from those present the previous year. Therefore, most SY males are exposed to songs different from the ones they eventually sing when they begin to breed. Given the importance of song conformity within a colony, there would be no advantage for SY males to develop crystallized song.

Fourth, cacique song serves no other social function that would make it beneficial for SY males to sing. For example young cooperatively breeding birds sometimes help defend group territories (Brown 1987). These young birds would be expected to develop crystallized song even though they may have little opportunity to breed.

Delayed vocal maturation is rare among songbirds probably because most birds have an opportunity to learn socially appropriate song before or during their second year, young territorial birds may have a small chance to breed in marginal habitat, and song production can be curtailed to avoid aggression.

Studies of vocal development in bellbirds have revealed interesting parallels with delayed vocal maturation in Yellow-rumped Caciques. D. E. Kroodsma (pers. comm.) believes that the songs of Three-wattled Bellbirds (*Procnias tricarunculata*) are learned, in

contrast to other suboscines in which song development has been investigated (Kroodsma 1984, 1985, 1989; Kroodsma and Konishi 1991). He observed predefinitive male bellbirds in a contact zone between two song dialects singing two distinct song variants, and recorded change over time in bellbird songs within a locality. These observations are not expected in species with innate song. Based on field observations of three bellbird species aged by plumage appearance (Bearded Bellbird, *Procnias averano*; White Bellbird, *P. alba*; and Three-wattled Bellbird), it appears that the second year of life is pivotal for song development (Snow 1970, 1973, 1977). During this year, males first begin to produce parrot-like squawks only slightly resembling the adult songs. They continue to produce these squawks for several months. Even by the end of the second year, the songs are distinguishable from adult songs as less ringing, shorter, irregular, or incomplete. More recently, D. E. Kroodsma (pers. comm.) has confirmed these findings with observations of color-banded Three-wattled Bellbirds of known age. However, it is unknown to what extent delayed vocal maturation in bellbirds parallels delayed song crystallization in caciques, since the timing of song learning in suboscines in general is not well understood.

Bellbirds breed in dispersed lek territories where males mate polygynously with females. During the breeding season, SY males sing or lurk silently near the boundaries of established territories, but do not possess their own (Snow 1977). Although mating success in bellbirds has not been measured, we speculate that, like young Yellow-rumped Caciques, predefinitive bellbirds may have almost no chance of obtaining a display territory or attracting a female.

Delayed maturation of song in Yellow-rumped Caciques and bellbirds differs from an example of delayed vocal development described for Brown-headed Cowbirds (*Molothrus ater*; O'Loghlen and Rothstein 1993). SY cowbirds from the Sierra Nevada Mountains had crystallized perch songs and flight whistles, but continued to modify their song repertoires until their third year. SY males used their songs to court females, albeit less successfully than adult males in this population (Rothstein et al. 1986). Prolonged song acquisition into the third year may allow cowbirds at high altitudes or latitudes, where the breeding seasons are short and opportunities for exposure to conspecific song limited, to add shared, local song types to their repertories (O'Loghlen 1995, O'Loghlen and Rothstein 2002).

Delayed vocal maturation has not been reported in three other highly polygynous icterid species, Boat-tailed Grackles (*Quiscalus major*; Poston et al. 1999), Great-tailed Grackles (*Q. mexicanus*; Johnson et al. 2000), and Montezuma Oropendolas (*Psarocolius montezuma*; Webster 1995) although details of vocal development and its timing likewise have not been reported. These species lack distinct, predefinitive plumages, and SY males were not always aged. Furthermore, genetic and behavioral evidence has shown that subordinate males attained some mating success by employing alternative mating strategies (Webster 1995, Poston et al. 1999, Johnson et al. 2000). It is not clear to what extent SY male caciques can take advantage of these alternative strategies.

While delayed vocal maturation is rare, further study of species in which vocal development is poorly known may uncover other examples. Based on our observations of Yellow-rumped Caciques, we would expect it to occur in birds in which young males have little opportunity for social success, particularly in polygynous species. Delayed vocal maturation should be less likely in species that mate and rear young in exclusive territories, where even young birds may have a chance to breed in marginal habitat.

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MOLT PATTERNS AND MOLTING GROUNDS OF LUCY'S AND VIRGINIA'S WARBLERS: SIMILAR YET DIFFERENT

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ABSTRACT.—Using museum specimens, we documented the molt cycles and molting grounds of adult Lucy's (*Vermivora luciae*) and Virginia's (*V. virginiae*) warblers. During prebasic molts, both species replace all body plumage. Prebasic primary molt takes a mean of 71 days for Lucy's Warblers, but a mean of just 42 days for Virginia's Warblers. Prebasic molt occurs exclusively on the breeding grounds. We found no evidence of a prealternate molt in Lucy's Warblers, and limited evidence of a prealternate molt in Virginia's Warblers. In both species, the seasonal change in crown color is a function of the freshly replaced gray-tipped feathers acquired during the prebasic molt being abraded during the winter, such that the basal red coloration of those same feathers is exposed during spring. These species differ from other western-breeding passerines in that they do not appear to directly exploit the late season food resources in the southwestern United States and northwestern Mexico. This difference is suggested by the lack of a shift from northern parts of their breeding range to molt in those potentially more productive regions of the southwestern monsoon region. The possibility of winter territoriality may play a role in the rapid prebasic molt exhibited by Virginia's Warblers. On the other hand, the lengthy prebasic molt of Lucy's Warblers may be explained by the use of poor nutritional resources during late summer, and/or the lack of territoriality during late summer and winter. We conclude that our data, in conjunction with data from previous studies, suggest multiple contrasting molt migration strategies among breeding passerines in western North America. *Received 4 September 2001, accepted 2 June 2002.*

Molt studies of birds which breed primarily in the western portions of North America have suggested interesting life history trade offs. The most widespread of these patterns is molt migration, which has been found in a number of diverse lineages (Rohwer and Manning 1990, Young 1991, Voelker and Rohwer 1998). Molt migration involves commencing the fall migration prior to the fall (prebasic) molt. This fall migration is then interrupted, as birds stop in the Sonoran and Chihuahuan desert regions of the southwestern United States and northwestern Mexico to begin molting. A stopover in this region allows molt-migrating species to avoid the late season droughts and corresponding loss of food availability on their breeding grounds, and to take advantage of food flushes produced in southwestern desert areas by late summer monsoon rains (Baldwin 1973, Rohwer and Manning 1990, Voelker and Rohwer 1998). The late summer monsoon region includes southeastern Colorado, eastern Arizona, New Mexico, the western extremes of Texas, the eastern two-thirds of Sonora, and all of Chihuahua, and extends southward into Mexico to at least 20° north latitude (Comrie and Glenn 1998).

This pattern of molt migration raises an interesting question: do birds that breed in the xeric western and southwestern portions of the United States, but winter farther south, also take advantage of the late summer increase in resource availability? If so, such western- and southwestern-breeding species should be concentrated in the molt migration area during some or all of their fall molting period. Evidence of such a pattern would be molting birds in species with disjunct breeding and wintering ranges that do not include the Mexican monsoon region being found predominantly in the molt migration area during their molts. Further, molting birds in species whose breeding or wintering ranges include portions of the Mexican monsoon region also should be concentrated in the monsoon region during molt.

This question was addressed initially by a study of molt in the Gray Vireo (*Vireo vicinior*; Voelker 2000). That study suggested that Gray Vireos do not take advantage of late summer resources by concentrating to molt in the molt migration stopover areas, and that they require a mean of 10 days longer to molt than do molt-migrating species. These results

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suggest the possibility that not only do molt-migrating species make use of desert food flushes, but that they also may be able to molt faster as a consequence.

In this paper we explore further the question of whether western- and southwestern-breeding species take advantage of late summer resource availability in molt migration areas by documenting the molting areas of Lucy's (*Vermivora luciae*) and Virginia's (*V. virginiae*) warblers. Both of these species breed throughout the western and southwestern United States, including portions of the molt migration area, and winter farther south along the western coast of Mexico. We also describe in detail the annual molt cycle of both species, including the seasonal color changes exhibited by *Vermivora* warblers.

METHODS

Study species.—Lucy's Warblers breed through southeastern California and along the southern third of the California-Nevada border, extreme southern Nevada, southern Utah, extreme southwestern Colorado, extreme northwestern New Mexico, north, west, and south Arizona excluding the extreme southwest, to southwestern New Mexico, the southwestern edge of Texas, extreme north and northeastern Chihuahua, northeastern Sonora, and extreme northeastern Baja California (Johnson et al. 1997, American Ornithologists' Union 1998). Breeding occurs most often in dense riparian mesquite (*Prosopis* spp.) woodlands, but habitats dominated by tamarisk (*Tamarix* spp.) also are used (Johnson et al. 1997). Lucy's Warblers winter from southern Sonora south to Oaxaca in a narrow strip along the Pacific coast and adjacent inlands, and sometimes along the central portion of the Texas-Chihuahua border (Johnson et al. 1997, American Ornithologists' Union 1998). Wintering habitat typically is restricted to dry washes, riparian gallery forests, and thorn scrub (Johnson et al. 1997). Winter territoriality has not been observed in these birds, and they are known to occur in mixed species flocks (Johnson et al. 1997). That portion of their breeding range which includes southeastern Arizona, southwestern New Mexico and Texas, and Chihuahua and Sonora is within the primary monsoon, or molt migration area, as are both the migratory range and the northern half of their wintering range (see Johnson et al. 1997, Comrie and Glenn 1998).

Virginia's Warblers breed throughout extreme southeastern California, Nevada excluding the northwest, southeastern Idaho, southern Wyoming, western South Dakota, Utah, Colorado excluding the east, Arizona except in the southwest and extreme west, New Mexico excluding the east, and into part of southwestern Texas. Breeding habitat includes pinon-juniper (*Pinus* spp. and *Juniperus* spp.) and oak (*Quercus* spp.) woodlands, dense mountain mahogany (*Cercocarpus* spp.), and brushy cover along streamsides (Olson and Martin 1999). Late in the breeding season Virginia's Warblers often are observed moving into low foothills (Phillips et al. 1964, Bailey and Niedrach 1965), and during migration they may depend strongly upon riparian corridors, where they often join mixed species flocks (Olson and Martin 1999). The winter range of Virginia's Warblers is from southern Nayarit and northern Jalisco south to southern Puebla and central Oaxaca (American Ornithologists' Union 1998, Olson and Martin 1999). Wintering habitat includes thorn scrub, and tropical deciduous, oak, and pine-oak woodlands (Olson and Martin 1999). Winter territoriality has not been reported. That portion of their breeding range which includes eastern Arizona, southeastern Colorado, New Mexico, and Texas is within the late summer monsoon region, as are both the migratory range and the northernmost portion of their wintering range (see Comrie and Glenn 1998, Olson and Martin 1999).

Scoring molt.—We examined 334 adult specimens of Lucy's and 287 adult specimens of Virginia's warblers from 28 museum collections (see acknowledgments). We used data from museum labels to determine gender, collection date, and collection locality of each specimen, and we used data from museum labels or plumage characters (see Pyle et al. 1997) to exclude hatching year birds from the analyses. We examined specimens under a 3× magnifying lamp lighted with a 22-watt fluorescent bulb, using a small forceps to lift feathers and quantify molt. We scored body molt by estimating the percentage of feathers growing in each of five regions: chin and throat, breast, belly, head, and back (definitions in Rohwer 1986). Percentage categories were 0, 10, 30, 50, 70, and 90% of feathers developing (Rohwer 1986). We summed the scores from the five regions and calculated a mean overall body molt score.

Both species have nine primaries and secondaries on each wing and 12 rectrices. To score flight feather molt, we followed Rohwer (1986) in estimating the fraction of the full length (by 0.1 intervals) each developing feather had reached, and scored missing feathers as 0. We used N to designate newly replaced feathers, and X to designate feathers not yet replaced on molting specimens (Voelker and Rohwer 1998). A hypothetical data sheet for a specimen replacing primaries on one wing reads: N, N, N, 0.9, 0.7, 0.3, 0, X, X, where primaries 1–3 are newly replaced and fully grown, primaries 4–6 are growing feathers, primary 7 is missing, and primaries 8–9 have yet to be dropped. The molt score for this wing is 4.9, where each N is scored as 1. Both wings of each specimen were examined and scored.

We generally followed Rohwer (1986) to determine whether molt was adventitious. However, we did score asymmetrical primary feather molt if one or more contiguous feathers were missing on one wing and not the other as long as the primary one was included in the missing feathers. We did this because primary molt often is not synchronized in these two species, with

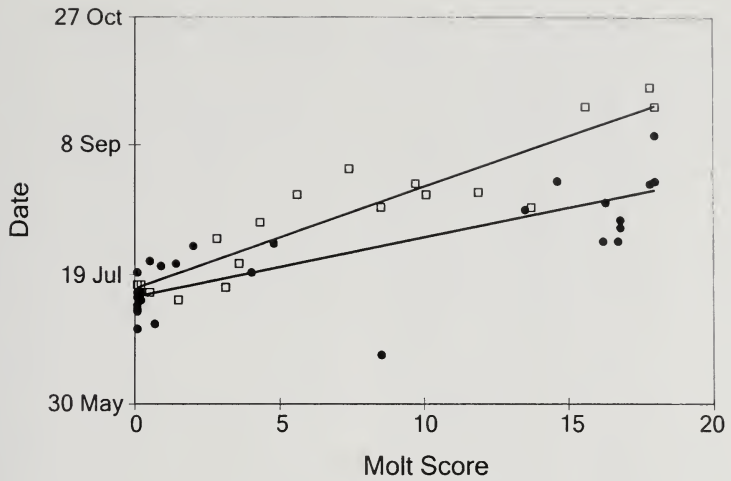

FIG. 1. Regression of collection date (Julian) over primary molt score, to estimate the time necessary to complete prebasic molt. Lucy's Warblers (*Vermivora luciae*; open squares) required a mean of 71 days to complete the prebasic molt ($y = 194.4[= 13$ July$] + 3.97X$, $r^2 = 0.85$, $n = 19$, $P < 0.001$), while Virginia's Warblers (*V. virginiae*; filled circles) required a mean of only 42 days ($y = 191.3[= 10$ July$] + 2.29X$, $r^2 = 0.66$; $n = 29$; $P < 0.001$). Data are from museum skins. See text for calculation of primary molt scores.

one wing beginning to molt slightly before the other (Voelker 2000).

We estimated the rate and duration of primary feather molt using Pimm's (1976) regression method, with date of collection (in Julian days) as the dependent variable and the summed score of growing and newly replaced primary feathers as the independent variable. The y intercept from the regression represents the mean molt initiation date. We calculated the mean molt completion date by replacing the x value from the regression equation with the maximum molt score value (here, 18), and solving Julian date. This method provides a mean estimate of primary molt duration for all individuals, and thus is more appropriate than reversing the axes, which is valid only when a single bird is followed through time (Pimm 1976, Langston and Rohwer 1996). Although all regression models for estimating molt are necessarily imperfect (Voelker 2000), Pimm's method is less so because it overcomes the problem of heteroscedasticity in molt data. All specimens that were molting primaries were included in the regression analyses.

We followed the molt terminology of Humphrey and Parkes (1959), and followed Langston and Rohwer (1996) in determining molt series (see Yuri and Roher 1997 for a detailed explanation of patterns of feather replacement and identification of molt series). Briefly, based on its stage of growth and the stage of growth of adjacent feathers, each developing feather can be categorized as nodal, terminal, or directional. Nodal feathers are replaced first in a series and are always closer to full length than adjacent feathers. Terminal feathers are replaced last in a series and are always less fully grown than adjacent feathers. The lengths of other developing feathers indicate whether the direction of feather replacement within a series proceeds proximally to distally, or distally to proximally.

RESULTS

Definitive prebasic molt.—Lucy's Warblers underwent prebasic molt from July through September (Fig. 1). Of the 36 specimens we examined from this period, 19 were molting. Virginia's Warblers were molting from June through September (Fig. 1). Of the 116 specimens we examined from this period, 29 were molting. All feathers in both species are replaced during the definitive prebasic molt; the primaries are replaced proximally to distally in a single series, beginning with P1 and ending with P9 (Table 1). P1 is always nodal, and was the only nodal feather for seven specimens of Lucy's Warblers and 14 specimens of Virginia's Warblers. However, four specimens of Lucy's Warblers and four specimens of Virginia's Warblers demonstrated that P2 also can be nodal, being dropped at the same time as P1 (Table 1). One specimen of Lucy's Warbler had dropped P1, P2, and P3 simultaneously. For three specimens of Lucy's Warblers and 12 specimens of Virginia's Warblers, P9 was the only terminal primary; one specimen of Virginia's Warbler had two terminal feathers, P9 and P8 (Table 1). The regression of collection date on primary molt score suggests

TABLE 1. Patterns of flight feather replacement in molting Lucy's (*Vermivora luciae*) and Virginia's (*V. virginiae*) warblers. Numbers in each column refer to the number of specimens in which each focal feather was being replaced. Nodal feathers are lost first in a molt series and indicate molt series initiation points, while terminal feathers are replaced last and indicate molt series completion points. Other growing feathers indicate directionality, which is determined by the condition of adjacent feathers relative to each focal feather. For both species, primary molt was initiated at primaries 1–3, proceeded proximally to distally (where each focal feather was not as far along in molt as the next most proximal feather, but farther along in molt than the next most distal feather) and terminated at primary 9. Secondaries were replaced in three or four series, as indicated by nodal feathers. Rectrices were replaced in one series. Data are from museum skins.

	Focal feather																							
Molt patterns	S9	S8	S7	S6	S5	S4	S3	S2	S1	P1	P2	P3	P4	P5	P6	P7	P8	P9	R1	R2	R3	R4	R5	R6
Lucy's Warbler (n = 18)																								
Proximal to distal molt			1					1			3	5	4	6	5	3	3			3	2	2	2	
Distal to proximal molt		1			2	2	2	1																
Nodal feathers		5	1	2					4	7	4	1							4					
Terminal feathers	3		1	2														3					1	4
Virginia's Warbler (n = 29)																								
Proximal to distal molt					2	7	5	4			6	3	3	3	1	6	8				1	1	1	
Distal to proximal molt																								
Nodal feathers		3		6					2	14	4								3					
Terminal feathers	1		1	7	10	2											1	12						4

primary replacement lasts a mean of 71 days in Lucy's Warblers, and 42 days in Virginia's Warblers (Fig. 1).

Secondary feathers are replaced in two, or possibly three, series for both species: S1 to S6 and S7 to S9, or S1 to S5, S6, and S7 to S9. The inner series is started first, at about the same time that P3 to P5 are being replaced. S8 generally is the nodal feather in this series (Table 1). However, one Lucy's Warbler had S7 as the nodal feather while S8 was scored as distal to proximal. S7 also was replaced after S8 but before S9, or at about the same time as S9. S9 always was terminal.

The outer secondary series is replaced distally to proximally (Table 1), with nodal feather S1 dropped at about the same time as P5 to P6. In all cases, S5 appears to be part of an S1 to S5 series. Therefore, S5 may in fact be the terminal feather of the distal secondary series. In one specimen of Virginia's Warbler, S4 also was a terminal feather. This distal secondary series generally is completed when the primary series is complete or shortly thereafter.

S6 may constitute its own molt series. In all cases where S6 was being replaced, S7 to S9 were fully grown, suggesting that S6 is not a part of that series. In 2 of 4 Lucy's Warblers and 6 of 13 Virginia's Warblers where both S6 and S5 were being replaced, S6 was more fully grown than S5, indicating that S6 was dropped first. Thus, S6 may not be part of the S1 to S5 series, at least in some individuals.

Rectrix molt begins about the time that P2 or P3 is dropped, and in both species is finished before primary feather molt is completed. In most specimens molting rectrices, feathers were replaced in a single series, with R1 as the nodal feather and R6 as the terminal feather. However, in 4 of 14 Lucy's Warblers and 3 of 12 Virginia's Warblers several rectrices were dropped at very nearly the same time, and in no apparent order (these seven specimens were not scored in Table 1).

Body molt overlaps primary molt in both species. In Virginia's Warblers, all five body regions appear to be molting by the time P2 to P3 are being replaced. All five regions are molting when P1 is replaced in Lucy's Warblers; therefore, body molt in Lucy's Warblers may begin slightly earlier.

Definitive prealternate molt.—We found just 9 of 84 specimens of Virginia's Warblers and 1 of 218 Lucy's Warblers collected between 1 January and 30 April to be molting. All nine specimens of Virginia's Warbers were molting body feathers, just six were replacing head feathers, and none were replacing flight feathers. This appeared to be a light body molt; only one specimen was molting in all five body regions and the highest overall body molt score was 24%. The single molting specimen of Lucy's Warbler was replacing body feathers on the chin and throat, and head regions (overall molt score of 12%).

Molt in relation to migration.—Every molting specimen of both species had been collected on the breeding grounds, and molting specimens were distributed throughout their breeding ranges. Further, we did not find birds in worn plumage on wintering grounds or in the migratory range during periods immediately following breeding. This strongly suggests that both species complete the prebasic molt on the breeding grounds before migrating to the wintering grounds, and that they are not making use of the southwestern monsoon region for molt.

DISCUSSION

Molt patterns.—Both Virginia's and Lucy's warblers replace their primaries in the pattern typical of most passerine species studied thus far. Several specimens from both species had S6 longer than S5 when both of these feathers were being replaced simultaneously. This pattern suggests that S6 is not a part of a single S1 to S6 series, but instead constitutes its own series. This pattern also is found in the Orange-crowned Warbler (*Vermivora celata*; Foster 1967), as well as in a number of New and Old world species from other genera (Jenni and Winkler 1994, Voelker 2000).

Rectrices in both species appear to be dropped in a single series, R1 to R6, and usually very rapidly. Four specimens of Lucy's Warblers and one specimen of Virginia's Warbler suggest that on occasion, rectrices are dropped so close in time that no pattern of replacement is apparent. This very rapid, nearly simultaneous loss of rectrices also has been documented in the Orange-crowned Warbler (Foster 1967). There is no evidence that R6 constitutes a molt series separate from R1 to R5, as has been documented in other recently

studied passerine species (e.g., Jenni and Winkler 1994, Voelker and Rohwer 1998, Voelker 2000).

We found no evidence of a prealternate molt in Lucy's or Virginia's warblers, yet both possess red crown patches which are evident to various extents during spring. Crown feathers acquired during the prebasic molt are mostly red, but have gray tips that mostly conceal the underlying red, and thus the crown patch. Therefore, the red crown patches apparent in these species during spring are the result of feather wear, in which the gray tips of these feathers wear away. This pattern of crown color change due to feather wear, suggested by Johnson et al. (1997) for Lucy's Warblers, also is evident in the Colima Warbler (*Vermivora crissalis*; Beason and Wauer 1998), and most likely occurs in the Orange-crowned Warbler as well (Foster 1967). As in Lucy's and Virginia's warblers, there appear to be a few individuals of Orange-crowned Warblers that undergo a prealternate molt (Foster 1967). Although quantitative data are lacking, the eastern race of the Nashville Warbler (*V. ruficapilla*) is presumed to replace head feathers during a prealternate molt, but with little resulting change in appearance (Curson et al. 1994). Because the newly replaced crown feathers in Nashville Warblers do in fact have gray tips which largely conceal the underlying red portion of the feathers, it is probable that red crown patches in this species also are the result of feather tip wear rather than feather replacement.

Timing of molt and migration.—Lucy's Warblers and Virginia's Warblers undergo the prebasic molt on the breeding grounds, as do almost all other *Vermivora* species (the *sordida* race of the Orange-crowned Warbler is the only known exception; Foster 1967, Curson et al. 1994, Beason and Wauer 1998).

Neither Lucy's nor Virginia's warblers perform a molt migration, i.e., they do not travel to a nonbreeding, nonwintering area to molt. They also do not concentrate in those portions of their breeding ranges which fall within the southwestern monsoon region. Performing molt migration is hypothesized to allow western North American species that breed in arid or in dry riparian habitats to take advantage of food flushes associated with late summer monsoons in southwestern United States and northwestern Mexican deserts (Szarek 1979, Nielson 1986). To date, four western species have been shown to perform such a molt migration (Bullock's Oriole, *Icterus bullockii*, Rohwer and Manning 1990; Western Painted Bunting, *Passerina ciris pallidior*, Thompson 1991; Lazuli Bunting *P. amoena*, Young 1991; and Western Warbling Vireo, *Vireo gilvus swainsonii*, Voelker and Rohwer 1998), and one species has been shown not perform it (Gray Vireo, Voelker 2000).

We had predicted that both Lucy's and Virginia's warblers would be taking advantage of late summer food flushes associated with monsoons in the southwestern United States and northwestern Mexico. This would be accomplished by moving away from northern and western portions of their breeding ranges, which presumably have lower resource availability during late summer. This presumption is due to the paucity of late summer rains in the northern and western portions of the breeding range of each species, compared to the rains associated with the monsoon region (Comrie and Glenn 1998). Therefore, we had expected to find one of two patterns. First, that molting specimens would be concentrated in the southern and southwestern portions of their range, as Bullock's Oriole has been shown to do (Rohwer and Manning 1990). The second possible pattern was that most molting specimens would have been collected outside of their breeding range, including the wintering grounds. This pattern was found in Painted Buntings (Thompson 1991). Either of these patterns would have suggested that these species were performing molt migration, and thus were likely taking advantage of late summer desert food flushes. Clearly, neither of these patterns is evident in Lucy's and Virginia's warblers, nor was either pattern evident in Gray Vireos, which breed in similar xeric regions of the United States (Voelker 2000).

There are several possibilities to explain why Lucy's and Virginia's warblers do not migrate away from their breeding grounds prior to molting. One is that they have sufficient resources for molt on their breeding grounds, making a molt migration unnecessary. This possibility was used to explain why the western-breeding Hermit (*Dendroica occidentalis*) and Townsend's (*D. townsendi*) warblers, which breed in more productive habitats, do

not perform a molt migration (Jackson et al. 1992).

Another possibility is that, given the relatively short distance between breeding and wintering ranges, these two species have sufficient time between breeding and migration to complete the prebasic molt. By comparison, species which migrate farther (such as molt migration species) may be forced by time constraints to molt someplace other than on the breeding grounds. Such time constraint arguments have been widely applied (Jenni and Winkler 1994), but generally overlook species or group specific patterns due to a lack of ecological comparisons between breeding and wintering ranges (Voelker 2000).

Indeed, such a "sufficient post breeding time" time constraint hypothesis is not a satisfying explanation for the observed molt duration differences between Lucy's and Virginia's warblers. Lucy's Warblers require a mean of 71 days to complete molt while Virginia's Warblers take just 42 days (Fig. 1). If this disparity was due to differences in breeding duration or breeding times, a difference would be expected in the mean molt initiation dates for the prebasic molt. However, the mean molt initiation dates are very similar for the two species, with most individuals of both species beginning to molt in mid-July. The difference lies in the mean molt completion dates, with Lucy's Warblers completing molt in late September, and Virginia's Warblers in late August (Fig. 1). This difference strongly suggests ecological or behavioral differences either in late summer on the breeding grounds, or on the wintering grounds, and thus potentially different constraints.

With respect to Lucy's Warblers, molt duration may be explained by wintering ecology and behavior. During winter, this species tends to form small flocks and occupy a habitat similar to that occupied on the breeding grounds (Johnson et al. 1997). Therefore, a lack of winter territoriality, and similarity of breeding and wintering habitats (and therefore potential similarity of food resources), could explain the comparatively prolonged molt period in this species; there may be no advantage of an increased molt rate. This explanation is different from that offered for the prolonged molt of Gray Vireos (Voelker 2000), which was attributed to the defense of winter territories and the associated late availability of winter food resources.

Notably, the mean length of molt for Lucy's Warblers is very similar to that of Gray Vireos (71 and 67 days, respectively), and the molt duration in these two species, neither of which is constrained to molt rapidly, is somewhat longer than the molt duration of species shown to perform a molt migration (54–57 days; Thompson 1991, Young 1991, Voelker and Rohwer 1998). This supports the hypothesis that molt-migrating species may be able to increase the rate at which the prebasic molt can be accomplished by making use of abundant resources (Voelker 2000). Further support of this idea is reflected in the seasonal diet of Lucy's Warblers, which switch to abundant but nutritionally poor food resources (leafhoppers) in July (i.e., when molt commences) after breeding is completed (Johnson et al. 1997). This suggests that the nutritional value of food is likely a key to the ability to molt more rapidly; it already is well documented that nutrition plays an important role in molt efficiency (Murphy and King 1992, Murphy and Taruscio 1995).

The short molt duration in Virginia's Warblers is more difficult to explain, largely because there is little information on its diet and wintering ecology (Olson and Martin 1999). One explanation might be that the difference in molt duration, compared to that of Lucy's Warblers, is due to a difference in the timing of migration. However, for migration timing differences to be a valid explanation in this case, Virginia's Warblers should depart the breeding grounds first. Instead, the opposite is true; Lucy's Warblers begin to leave the breeding grounds a full month before Virginia's Warblers (Johnson et al. 1997, Olson and Martin 1999).

Alternatively, Virginia's Warblers are difficult to detect on the breeding grounds by late July; it has been suggested that they disperse to lower elevations (and thus to potentially different habitats) before the onset of migration, which peaks in August (Phillips et al. 1964, Bailey and Niedrach 1965). Thus it is possible that breeding habitats have low resource availability during late summer, and that Virginia's Warblers may be changing to more productive habitat associations, such as riparian corridors (albeit still within the limits

of the geographic breeding range) during the molt period. Therefore, the comparatively rapid molt in this species may be attributable to the availability of abundant, late season, high nutrition resources within the breeding range.

The possibility of winter territoriality or winter food resource defense in Virginia's Warblers should not be ruled out as causal factors of a rapid molt. The need to establish and maintain winter territories certainly could drive the evolution of a very rapid molt. That this molt occurs on the breeding grounds suggests the possibility that resources on such a wintering territory may not be abundant enough, or may not be of sufficient nutritional value to support regular daily maintenance, the costs associated with replacing feathers, and the costs of territorial defense, as has been argued elsewhere (Voelker 2000).

We predict that a study of the nonbreeding ecology of Virginia's Warblers would establish one of the above possibilities (availability of late season resources within the breeding range, or winter territoriality) as the mechanism of the rapid molt we detected in this study. We conclude that there does not appear to be a single unifying pattern of molt migration or resource use among western-breeding passerine species; only if numerous species specific molt studies are conducted will we be able to determine whether few or many patterns exist with respect to molt and migration. This study and others highlight the potential loss of information inherent in time constraint models, if such models are themselves based on generalized observations of molt rather than on well-documented patterns within individual species. Finally, we contend that studies of wintering ecology, and the collection of data from nonbreeding specimens, are still desperately needed to aid in unraveling the interplay among different life history aspects of many common species.

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AGE-RELATED DIFFERENTIAL TIMING OF SPRING MIGRATION WITHIN SEXES IN PASSERINES

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ABSTRACT.—We examined differential timing of spring migration by age class for passerines banded at Long Point Bird Observatory from 1984 to 1998. Mean capture dates of after-second-year (ASY) males were earlier than second-year (SY) males for 19 of 20 species, 16 significantly so. Mean capture dates of ASY females were earlier than SY females for 11 of 12 species, 8 significantly so. There was no significant difference in the timing of migration between age classes for males of species with highly distinctive SY plumages and males of other species with more subtle plumage differences between age classes. For 12 species with adequate samples of both sexes, the mean difference in capture dates between age classes was significantly greater for males (3.5 days) than for females (2.1 days). These results suggest that differential migration by age class is widespread among passerines and that factors leading to the delayed arrival of young males also may affect females, though to a lesser extent. *Received 15 May 2001, accepted 31 January 2002.*

In many species of birds, males precede females on spring migration (Francis and Cooke 1986, 1990; Lozano et al. 1996; Swanson et al. 1999). Exceptions include species with polyandrous mating systems where females tend to be the dominant sex and precede males on spring migration (Oring and Lank 1982, Reynolds et al. 1986). Several possible factors have been suggested to explain these patterns. Sexual selection on the breeding grounds could lead to the sex that experiences the greatest amount of intrasexual competition for territories and/or mates arriving earlier. Related to this, the larger sex may be better able to tolerate harsh conditions early in the season (Ketterson and Nolan 1976, 1979). Intersexual competition for limited food resources on the wintering grounds could lead to the dominant sex excluding the subordinate sex from either (1) northerly wintering grounds, which would allow the dominant individuals to winter closer to the breeding grounds, thus facilitating their earlier arrival (Ketterson 1979, Ketterson and Nolan 1979), or (2) habitats with better food supplies, which would decrease the subordinate sex's physical condition and delay their departure (Marra and Holberton 1998, Marra et al. 1998). Francis and Cooke (1990) suggested that these hypotheses are not mutually exclusive because selection for early arrival on the breeding grounds also could affect wintering ground choice and size dimorphism.

Less is known about the differential timing between age classes within each sex during spring migration. Differences in shape and color pattern between the feathers of younger (second-year or SY) North American passerines that retain their juvenile primaries, rectrices, and selected wing coverts, and those of older (after-second-year or ASY) birds only recently have been described for a wide range of species (Pyle et al. 1987, Pyle et al. 1997). Thus, many previous analyses of differential migration by age class have been restricted to species that have striking differences in plumage color between SY and ASY individuals (Rohwer and Niles 1979, Flood 1984, Francis and Cooke 1986, Hill 1989, Francis and Cooke 1990, Morton and Derrickson 1990). In these cases, ASY males migrate earlier than SY males.

However, in all but about 35 North American passerines, ASY and SY males have similar plumage coloration (Rohwer and Butcher 1988), hence the differential migration patterns of species with different ASY and SY

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plumages may not be typical of other species. Rohwer et al. (1980) suggested that some SY males have female-like plumage to reduce aggression from ASY males and subsequently gain breeding opportunities. They predicted that SY males with female-like plumage should arrive at the breeding grounds after ASY males whereas SY males with ASY-like plumage should arrive at the same time as ASY males.

Nevertheless, a tendency for SY males to arrive after ASY males has been shown for a number of other passerine species which do not show striking plumage differences between age classes, many of which are summarized by Hill (1989). Both Rohwer et al. (1980) and Hill (1989) have suggested that species without a distinct SY plumage show a greater overlap in ASY and SY spring arrival dates than species with distinct plumage differences between ASY and SY males. However, the methodology used to determine ASY and SY male spring arrival dates varied greatly among studies, ranging from observations of first territorial behavior on the breeding grounds (Stewart 1973, Wittenberger 1978, Eliason 1986, Hopp et al. 1999) to determining ASY and SY passage dates from museum collection dates (Johnson 1965, 1973) or from specimens collected from tower kills during migration (Nolan and Mumford 1965). In some studies age was not recorded, but differential migration between age classes was inferred based on relationships between wing chord and migration dates (Hussell 1981, Bédard and LaPointe 1984, Francis and Cooke 1986). A more consistent approach is needed to test whether the tendency of ASY males to migrate earlier than SY males is typical of passerines without distinct plumage differences between age classes and to test whether ASY and SY males of these species show less difference in their migration dates than males of other species with distinct SY male plumages.

Even less is known about age specific differences in migratory timing of females, largely because age classes generally are more difficult to distinguish. In both Purple Martins (*Progne subis*) and Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*), ASY females arrive at the breeding grounds earlier than SY females (Crawford 1978, Morton and Derrickson 1990). Francis and Cooke (1990) inferred that SY female Rose-breasted Grosbeaks (*Pheucticus ludovicianus*) arrived later than ASY females based on a trend for later migrants to have shorter wing lengths, but the females in their sample were not aged.

We examined mean capture dates of 20 species of passerines captured and banded during spring migration at Long Point Bird Observatory (LPBO) from 1984 to 1998 to test whether older, ASY males migrate before younger, SY males in species with and without distinct plumage differences between male age classes and to test whether ASY females migrate before SY females.

METHODS

Capture data.—We captured birds using a combination of mist nets and Heligoland traps at three stations on Long Point, Ontario, Canada (42° 33′ N, 80° 10′ W), on the north shore of Lake Erie. Spring trapping was carried out daily, weather permitting, from early April to the beginning of June, 1984–1998. Further details of the banding and migration monitoring operations are described in Francis and Hussell (1998) and Dunn (2000).

We pooled data from all three banding stations over the 14-year period. We used data from all passerine species captured on spring migration that could be sexed and aged reliably (Pyle et al. 1997) and for which $\geq$50 known age birds of a particular sex, with $\geq$10 in each age class, were banded. We excluded any species-sex combinations for which aged birds constituted $<$35% of the total birds captured for that sex of that species. We also excluded species that had substantial local breeding populations around the banding stations, such that many individuals captured may have been local breeders captured well after their initial arrival dates.

To test whether differences in migration dates between age classes of males were related to plumage differences, we classified species into three groups according to the plumage differences (or lack of) between ASY and SY males (Table 1). The first group included only the American Redstart (*Setophaga ruticilla*), in which SY males have a gray and yellow plumage resembling females, rather than the black and orange of ASY males. The second group consisted of species in which the SY males differ conspicuously from ASY males (e.g., by brown instead of black primaries often with substantially less bright colors elsewhere on the body), but do not resemble females. The third group consisted of the remaining species which have relatively subtle differences, in which the age classes are distinguished mainly by differences in shape, wear, or edging of the primary coverts, primaries, or rectrices.

Although mean capture dates varied among years

TABLE 1. Mean capture dates ± SE (*n*) for after-second-year (ASY) and second-year (SY) passerines, plus birds of unknown age, captured at Long Point Bird Observatory during spring migration, 1984–1998. Dates begin April 1 (e.g., May 3 = 33). Lines indicate insufficient data for analysis. Species were classified according to the plumage differences between male age classes: D = dichromatic, where SY males have distinct subadult plumage resembling females; S = somewhat dichromatic, where SY males differ conspicuously from ASY males but do not resemble females; N = no difference, where SY males closely resemble ASY males and are distinguished from ASYs by feather wear and shape.

Species	Plumage	Males	
		ASY	SY
Tennessee Warbler (*Vermivora peregrina*)	N	44.5 ± 0.4 (50)	47.7 ± 0.7 (39)
Nashville Warbler (*Vermivora ruficapilla*)	N	38.5 ± 0.6 (87)	41.3 ± 0.4 (160)
Chestnut-sided Warbler (*Dendroica pensylvanica*)	N	46.0 ± 0.6 (100)	50.1 ± 0.4 (250)
Magnolia Warbler (*Dendroica magnolia*)	N	46.9 ± 0.2 (970)	50.4 ± 0.2 (1516)
Cape May Warbler (*Dendroica tigrina*)	N	42.7 ± 0.5 (62)	44.6 ± 0.7 (53)
Black-throated Blue Warbler (*Dendroica caerulescens*)	N	41.1 ± 0.6 (115)	45.5 ± 0.3 (155)
Yellow-rumped Warbler (*Dendroica coronata*)	N	30.7 ± 0.4 (297)	33.6 ± 0.2 (1040)
Black-throated Green Warbler (*Dendroica virens*)	N	40.5 ± 1.3 (46)	47.2 ± 0.9 (123)
Blackburnian Warbler (*Dendroica fusca*)	N	46.5 ± 0.8 (48)	50.0 ± 0.8 (63)
Bay-breasted Warbler (*Dendroica castanea*)	N	45.3 ± 0.6 (43)	49.0 ± 0.6 (62)
Blackpoll Warbler (*Dendroica striata*)	N	52.8 ± 1.4 (12)	54.7 ± 0.6 (59)
Black-and-white Warbler (*Mniotilta varia*)	N	35.7 ± 0.4 (231)	38.8 ± 0.4 (300)
American Redstart (*Setophaga ruticilla*)	D	47.0 ± 0.3 (305)	52.1 ± 0.4 (314)
Canada Warbler (*Wilsonia canadensis*)	N	51.0 ± 0.5 (91)	54.3 ± 0.6 (128)
Scarlet Tanager (*Piranga olivacea*)	S	41.2 ± 0.7 (36)	45.8 ± 0.7 (59)
Eastern Towhee (*Pipilo erythrophthalmus*)	S	21.2 ± 1.5 (44)	25.2 ± 0.7 (203)
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	S	39.7 ± 0.3 (261)	43.1 ± 0.3 (337)
Indigo Bunting (*Passerina cyanea*)	S	49.6 ± 3.0 (11)	48.5 ± 0.7 (80)
Brown-headed Cowbird (*Molothrus ater*)	N	26.1 ± 1.8 (81)	28.5 ± 1.4 (129)
Baltimore Oriole (*Icterus galbula*)	S	43.4 ± 0.5 (204)	47.4 ± 0.4 (366)

[a] Probability that the observed difference between mean ASY and SY passage dates is due to chance (Wilcoxon 2-sample test).

(e.g., due to weather conditions), capture dates were not standardized to year because the effects of weather are complex, affecting timing differently throughout the season, and also interact with both differences in trapping efforts as well as differences in population arrival (Francis and Cooke 1986). In addition, sample sizes for many species were relatively small in individual years. As few birds of most passage migrants were recaptured on subsequent days, we assumed that capture dates provide a good approximation of passage dates.

Some species included a high percentage of unknown age birds, which could lead to bias if the sample of aged birds was not representative. There are several reasons why birds may not be aged: failure to record the information, lack of knowledge or lack of experience with the aging criteria by the bander, or difficulties in deciding because the characters appear intermediate, especially for species differing in subtle characters. To test whether the sample of known age birds might be biased, we also estimated mean capture dates of unknown age birds, and tested whether differences between age classes were related to the proportion of unknown age birds.

Statistical analyses.—We based comparisons among age-sex groups on mean dates, which give greater precision than median dates, but used Wilcoxon 2-sample tests for statistical comparisons to minimize the influence of unusually early or late arrivals on the tests. A sequential Bonferroni adjustment (Rice 1989) was made following the Wilcoxon 2-sample tests to reduce the possibility of committing a type 1 error. We used both a Spearman rank correlation and analysis of variance to test whether differences in migration dates between ASY and SY males were related to their classification based on plumage differences. We used a signed rank test to test whether the difference between age classes for males differed from that for females of the same species, for species with adequate samples of both sexes. We also used regression analysis and analysis of covariance to test whether differences between sexes or age classes differed for early-arriving and late-arriving species.

RESULTS

Adequate samples that met our criteria for inclusion were available for males of 20 species (8,456 known age individuals) and for females of 12 species (2,972 known age individuals). With the exception of the Indigo Bunting (*Passerina cyanea*), in which ASY males were captured slightly later than SY

TABLE 1. EXTENDED

Males		Females			
Unknown	P^a	ASY	SY	Unknown	P^a
47.6 ± 0.6 (87)	0.0001	48.1 ± 0.6 (51)	50.6 ± 0.8 (48)	52.0 ± 0.5 (133)	0.0395
40.7 ± 0.3 (438)	0.0003	43.3 ± 0.4 (75)	44.4 ± 0.5 (114)	45.6 ± 0.3 (338)	0.1295
46.4 ± 0.4 (297)	0.0000	50.4 ± 0.7 (71)	52.8 ± 0.7 (110)	50.7 ± (188)	0.0029
48.9 ± 0.2 (857)	0.0000	51.4 ± 0.3 (371)	53.9 ± 0.2 (984)	53.0 ± (643)	0.0000
43.1 ± 0.8 (60)	0.1263	46.0 ± 0.8 (39)	47.5 ± 0.5 (78)	49.3 ± 0.4 (131)	0.0266
44.6 ± 0.8 (41)	0.0000	—	—	—	—
32.9 ± 0.5 (321)	0.0000	40.3 ± 0.6 (135)	41.8 ± 0.4 (353)	40.6 ± (636)	0.0336
41.5 ± 1.0 (127)	0.0000	48.0 ± 1.2 (37)	52.8 ± 0.8 (78)	40.3 ± 0.8 (117)	0.0044
48.4 ± 0.7 (72)	0.0084	52.1 ± 1.0 (33)	56.4 ± 0.8 (65)	55.4 ± 0.6 (131)	0.0026
48.9 ± 0.5 (80)	0.0000	49.6 ± 1.0 (21)	50.1 ± 0.9 (30)	52.6 ± 0.6 (85)	0.1788
54.5 ± 0.7 (81)	0.1565	60.5 ± 1.4 (18)	58.2 ± 0.8 (51)	60.0 ± 0.6 (81)	0.1709
39.8 ± 0.7 (113)	0.0000	—	—	—	—
47.6 ± 1.0 (19)	0.0000	—	—	—	—
52.1 ± 0.4 (253)	0.0001	54.3 ± 1.0 (38)	57.9 ± 0.5 (88)	56.0 ± 0.4 (216)	0.0002
50.0 ± 0.7 (4)	0.0000	—	—	—	—
23.3 ± 1.8 (27)	0.0460	30.4 ± 1.3 (49)	32.3 ± 2.3 (35)	32.0 ± 0.8 (123)	0.1924
40.0 ± 1.2 (25)	0.0000	—	—	—	—
48.5 ± 1.6 (40)	0.8883	—	—	—	—
32.6 ± 3.0 (22)	0.0648	—	—	—	—
48.2 ± 1.3 (56)	0.0000	—	—	—	—

males (difference was not significant: P = 0.89), ASY males were captured earlier than SY males for 19 of the 20 species, 16 of them significantly so (P values <0.05; Table 1). With the exception of the Blackburnian Warbler (*Dendroica fusca*; P = 0.008) and the Eastern Towhee (*Pipilo erythrophthalmus*; P = 0.046), all other significant differences between ASY and SY passage dates remained significant following sequential Bonferroni adjustment (α = 0.0083).

The difference in capture dates for male American Redstarts, with their female-like SY male plumage (5.1 days), was the second highest among all species (the Black-throated Green Warbler, *Dendroica virens*, showed the greatest difference, 6.7 days), but the mean for other species with distinctive male SY plumages (mean ± SE: 3.0 ± 1.0 days) was slightly less than that for species with more subtle differences between SY and ASY males (3.5 ± 0.2 days). The difference between groups was not significant based on either a rank correlation (r_s = 0.28, P = 0.23), or analysis of variance ($F_{2,19}$ = 0.81, P = 0.46).

Among females, ASYs were captured earlier than SYs for 11 of the 12 species examined, 8 significantly so (P values <0.05; Table 1). The only exception was the Blackpoll Warbler (*Dendroica striata*) for which ASY females were captured slightly later than SY females, but the difference was not significant (P = 0.18). With the exceptions of the Tennessee Warbler (*Vermivora peregrina*; P = 0.040), the Cape May Warbler (*D. tigrina*; P = 0.027), and the Yellow-rumped Warbler (*D. coronata*; P = 0.034), differences between ASY and SY female passage dates remained significant following sequential Bonferroni adjustment (α = 0.007).

To compare differential migration of males and females, we restricted analysis to those 12 species with adequate samples for both sexes. The mean difference between age classes was significantly larger for males than for females (males: 3.46 ± 0.36; females: 2.05 ± 0.50

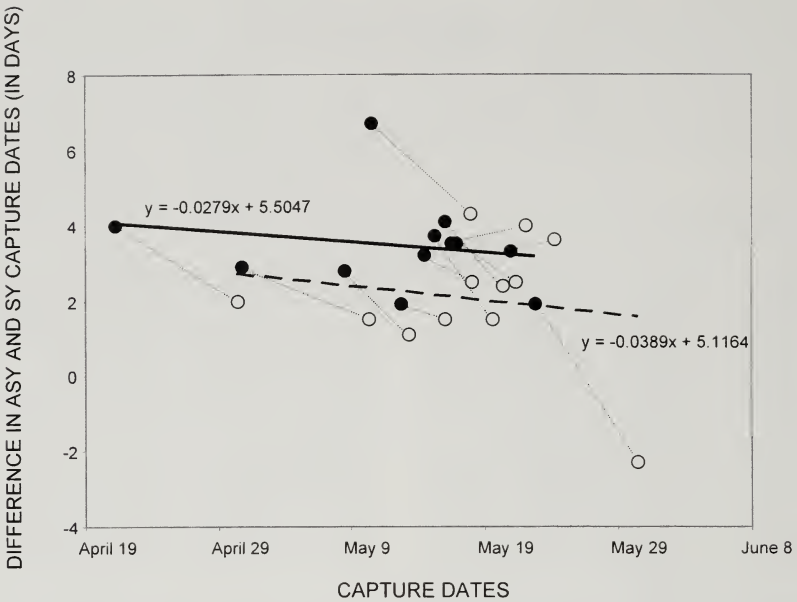

FIG. 1. The difference in capture dates between age classes in 12 passerine species was significantly greater for males (solid circles, solid line) than for females (open circles, dashed line) captured at Long Point Bird Observatory during spring migration 1984–1998, even after correcting for a tendency for differences to decline over the season. Points representing males and females of the same species are joined together by light dotted lines. See Table 1 for list of species.

days; Wilcoxon paired test, $Z = 2.74$, $P = 0.006$). Previous studies have shown that species that migrate earlier in the season have greater differences in migration dates between males and females than later migrating species (Francis and Cooke 1986), and the same pattern was apparent for the 12 species in this study (regression of difference in capture dates between ASY males and ASY females against mean capture date of ASY males; b = −0.16, SE = 0.06, $r^2 = 0.40$, $P = 0.026$). Thus, we tested whether the smaller differences between age classes of females could be related to their later arrival. Within each sex, there was a slight tendency for a reduced difference in capture dates between age classes later in the season, but it was not significantly different from zero in either case (males: b = −0.03, SE = 0.04, $r^2 = 0.04$, $P = 0.54$; females: b = −0.04, SE = 0.07, $r^2 = 0.03$, $P = 0.60$). The mean difference in arrival dates between age classes of females was still about 1.2 days less than that of males even after adjusting for differences in arrival dates (Fig. 1).

Mean capture dates for birds of unknown age were intermediate between those of known ASY and SY birds for males in 16 of 20 species and for females of 8 of 12 species (Table 1). This suggests that for most species, the unknown birds were a mixture of both age classes. In the 8 exceptions, birds of unknown age tended to be later than SY birds, but this was significant in only two cases: female Nashville ($P = 0.017$) and Cape May warblers ($P = 0.0007$). In neither sex was there a significant relationship between the proportion of unaged birds and the difference between age classes (males: $r = -0.19$, $n = 20$, $P = 0.43$; females: $r = -0.12$, $n = 12$, $P = 0.70$).

DISCUSSION

ASY male passage dates preceded SY male passage dates for most species regardless of whether the species showed distinct plumage differences between male age classes. Thus, delayed arrival time of young birds does not appear to be associated with delayed plumage maturation. Instead, differential migration by age class appears to be widespread among passerines.

Several hypotheses have been proposed to

explain the late migration of SY males relative to ASY males. SY males may be energetically constrained to arrive later, possibly due to dominance interactions on the wintering grounds. Marra et al. (1993, 1998) found that ASY male American Redstarts excluded SY males from high quality foraging habitat during winter; consequently, SY males that occupied lower quality habitats were in reduced physical condition and departed from the wintering grounds later than individuals that occupied higher quality habitats. Even if SY males are able to depart for the breeding grounds at the same time as ASY males, SYs might not be able to withstand the harsh conditions at the breeding grounds during early spring. On the other hand, SY males may not benefit from arriving too early, particularly if later-arriving ASY males are able to usurp territories from SY males (Morse 1973, Howe 1974, Sherry and Holmes 1989). If SY males have little to gain by arriving early, they may instead benefit by arriving later, thus avoiding the energetic costs of competition and aggression from older males (Hill 1989), as well as risks associated with poor weather (Whitmore et al. 1977) or low food supplies (Nolan 1978, Lank et al. 1985) early in the season. Given that many Neotropical migrants that do not show age dichromatism are subject to similar constraints on both the wintering and breeding grounds as species that do have distinct ASY and SY plumages (Rappole and Warner 1980, Greenberg 1986, Holmes et al. 1989, Wunderle 1995), differential migration by age class should not be unexpected for these species.

In females also, there was a tendency for ASYs to arrive earlier than SYs. Like males, females may be subject to intrasexual competition for breeding resources (Krebs 1971, von Haartman 1971). They also may be subject to competition for territories and food resources on the wintering grounds (Rappole and Warner 1980, Greenberg 1986, Holmes et al. 1989). Thus, the selective pressures and other factors that have been proposed to affect arrival times of males also are likely to affect females. However, the difference between ASY and SY female mean capture dates was significantly less than the difference between ASY and SY male mean capture dates, suggesting these pressures are weaker for females. This could be related to male-biased sex ratios on the breeding grounds. For example, in a two-year study of a Baltimore Oriole (*Icterus galbula*) population, Flood (1984) found that there were considerably fewer females than males during both years and that all females and adult males bred, while only a third of the SY males bred. Male-biased sex ratios also are suggested by the disproportionately higher numbers of male floaters than female floaters in songbird populations (Arvidsson and Klaesson 1984, Sherry and Holmes 1989), and possibly higher mortality rates of females than males (Sherry and Holmes 1989, Woolfenden et al. 2001). As a result, females may be more likely to find a mate, regardless of arrival dates, though not necessarily the best quality male. Thus, the pressure to migrate early may not be as strong for females as it is for males. Also, differences in quality between winter territories of SY and ASY males could be greater than those between SY and ASY females if males are more strongly aggressive or territorial during winter. This could lead to greater differences between age classes for males than females in departure dates from wintering grounds, and thus migration dates.

In this study, the large percentage of unaged birds in some species could bias our conclusions if the aged birds are not representative of the population. However, our analyses indicate that for most species, the unaged birds appeared to be a mixture of both age classes, as would be expected if the aged birds are a representative sample. Furthermore, there was no evidence of a relationship between the proportion of unaged birds and the difference between age classes in migration dates. Thus, although unaged birds could certainly bias analyses of other parameters, such as age ratios, our analyses of differences in migration timing appear to be robust to this problem.

In summary, age-related differential migration in both sexes appears to be widespread among passerines. The constraints that affect passage dates in males with striking plumage differences between age classes apparently similarly affect species with more subtle male plumage differences. There were greater differences between ASY and SY male passage dates than between ASY and SY female pas-

sage dates, which suggests that these factors also may affect females, but to a lesser extent.

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Age and Sex Differences in Wing Loading and Other Aerodynamic Characteristics of Merlins

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ABSTRACT.—We examined age and sex differences in wing loading, aspect ratio, and wing span in a sample of 208 Merlins (*Falco columbarius*) captured at Cedar Grove, Wisconsin, during fall migration, 1978–1993. We also examined differences in tail loading of 166 of these Merlins. Adult males had significantly greater mass and wing loading than juvenile males. Adult females differed significantly from juvenile females only in mass. Females were significantly greater than males in every measure except aspect ratio. There were no apparent age differences in tail area or flight surface loading, but females had greater values in both. Merlins show fewer age differences in aerodynamic characteristics than Sharp-shinned Hawks (*Accipiter striatus*), probably because of differences in how the two species pursue and capture avian prey. Merlins usually capture prey in the air, sometimes after multiple stoops and at high flight speeds. In contrast, Sharp-shinned Hawks take birds from their perch or after a brief chase, often in dense vegetation, at relatively low flight speeds. Slower flight speeds require larger control surfaces and can explain the increased age differences in wing and tail areas in Sharp-shinned Hawks.

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Wing area, wing loading, and other aerodynamic characteristics are especially important for those diurnal birds of prey which spend considerable time on the wing and rely on agility in flight for the capture of prey. Adult Sharp-shinned Hawks (*Accipiter striatus*) have significantly greater wing lengths, wing widths, aspect ratios, wing areas, mass, and wing loadings than juveniles, and all of these measures are significantly greater in females than in males (Mueller et al. 1981). Brown and Amadon (1968) summarized the data on wing loading available for Falconiformes: measurements of wing loadings were available for only 56 species, half of these were represented by samples of only one, both sexes were measured for only seven species, and age was not noted for any. Since that time, data for both sexes have been published for only six species. Only one sample of wing loading for each sex was reported for the Ferruginous Hawk (*Buteo regalis*), the Red-tailed Hawk (*B. jamaicensis*), and the Swainson's Hawk (*B. swainsoni*; Janes 1985). Marsh and Storer (1981) reported wing loadings for 21 male and 24 female Cooper's Hawks (*A. cooperii*), and Jenkins (1995) provided wing loadings for 13 male and 20 female Peregrine Falcons (*Falco peregrinus*) and 20 male and 20 female Lanner Falcons (*F. biarmicus*). Age of the birds was not indicated in any of the three studies. Amadon (1980) compared the areas of juvenile and adult raptors (primarily wing and tail length) and found that in the smaller falcons (including the Merlin) juveniles "are smaller or about the same as the adult." This leads to a prediction that age differences in wing loading and other characteristics in Merlins would be less than that of Sharp-shinned Hawks. In this paper we examine age and sex differences in wing loading and other aerodynamic characteristics of Merlins (*F. columbarius*) based on a sample of 208 wings and 166 tails.

STUDY AREA AND METHODS

We captured Merlins during fall migration, 1978–1993, at the Cedar Grove Ornithological Station (43° 33′ N, 87° 21′ W) on the western shore of Lake Michigan in Sheboygan County, Wisconsin. The methods used to obtain the data are explained in detail in Mueller et al. (1981). Briefly, the extended wing (or tail) was held up against a vertical sheet of Plexiglas ruled into 5-cm squares and photographed. The negatives

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TABLE 1. Wing area, wing loading, and other characteristics of Merlins (*Falco columbarius*) captured at Cedar Grove, Wisconsin, during fall migration, 1978–1993.

	Adult males (n = 57)		Juvenile males (n = 52)		Adult females (n = 49)		Juvenile females (n = 50)	
Measurements	mean	SD	mean	SD	mean	SD	mean	SD
Wing chord (cm)	19.3	0.40	19.1	0.52	21.3	0.40	21.2	0.38
Wing length (cm)	25.7	0.72	25.5	0.79	28.6	0.96	28.3	0.96
Wing width (cm)	7.5	0.33	7.6	0.29	8.5	0.32	8.5	0.42
Wing span (cm)	57.0	1.44	57.7	1.47	63.7	1.99	63.3	1.76
Aspect ratio	7.64	0.33	7.56	0.20	7.50	0.33	7.27	1.40
Wing area (cm^2)	425.9	22.42	441.2	21.81	542.6	33.60	537.9	46.65
Mass (g)	160.2	8.76	153.6	9.74	222.4	13.75	212.3	12.41
Wing load (g/cm^2)	0.373	0.03	0.348	0.02	0.405	0.03	0.400	0.04

later were projected to life size and an outline drawn of the wing (or tail). We measured the area of the drawing with a compensating polar planimeter. Measurements were taken as in Mueller et al. (1981) except for the following: (1) wing area was twice the area of one wing plus the area of the body adjacent to the wing, and (2) aspect ratio was the square of wing span divided by wing area. We aged the falcons by plumage (Sodhi et al. 1993) and we sexed juveniles by size. The mean wing chord of 618 juvenile Merlins sexed as males at Cedar Grove was 192.06 ± 3.56 SD and of 648 sexed as females was 212.63 ± 4.04 SD, indicating that >99% of the birds could be sexed correctly by wing chord alone. We performed statistical tests with SYSTAT (Wilkinson 1989) on a Macintosh G3 computer. We used t-tests for independent samples for all comparisons.

The tails of the falcons were spread to varying degrees and the areas varied accordingly. Estimates were necessary to standardize tail area. We used the following formula to estimate tail area:

$$\text{Area} = (A/360)(\pi B^2 - \pi C^2),$$

where A is the angle formed by lines drawn along the two outer rectrices until they meet on a drawing made from a photograph of the tail, B is the distance from the apex of this angle to the tip of the longest rectrix, and C is B minus the tail length measured on the live bird. Unlike for Sharp-shinned Hawks (Mueller et al. 1981), this formula was a better fit than one using the sine of the angle and the length of the tail (r = 0.95 and r = 0.89, respectively). A folded tail of a Merlin probably is held at an angle of 10° and a spread of 110° probably is the maximum possible without gaps between the rectrices. Statistical tests of significance were not used to compare tail areas because those estimates were derived.

RESULTS AND DISCUSSION

Juvenile males had greater wing widths and wing areas than adult males, but neither difference was significant (Tables 1 and 2). Adult males had a greater wing chord, wing length, aspect ratio, mass, and wing loading than juvenile males, but only the last two differences were significant. Adult females were larger than juvenile females in all of the above measures, but only the difference in mass was significant. Females were considerably larger than males and differed significantly in every individual measurement. The sex difference in

TABLE 2. Age and sex comparisons of Merlins (*Falco columbarius*) captured at Cedar Grove, Wisconsin, during fall migration, 1978–1993. Means and standard deviations are presented in Table 1.

	Age comparisons				Sex comparisons			
	Males (df = 107)		Females (df = 97)		Adults (df = 104)		Juveniles (df = 101)	
Measurements	t	P	t	P	t	P	t	P
Wing chord	1.43	0.16	0.31	0.19	26.40	0.00	23.26	0.00
Wing length	1.68	0.10	1.60	0.11	17.39	0.00	25.48	0.00
Wing width	1.53	0.13	0.75	0.45	16.05	0.00	11.58	0.00
Wing span	1.98	0.05	0.23	0.82	19.20	0.00	14.79	0.00
Aspect ratio	2.77	0.08	0.25	0.81	2.35	0.03	0.23	0.82
Wing area	0.23	0.82	1.25	0.22	21.47	0.00	14.98	0.00
Mass	3.71	0.00	3.68	0.00	28.47	0.00	26.74	0.00
Wing load	2.92	0.00	1.62	0.11	6.61	0.00	7.00	0.00

TABLE 3. Estimated tail area of Merlins (*Falco columbarius*) captured at Cedar Grove, Wisconsin, during fall migration 1978–1993.

	n	Tail length (cm)	Area (cm^2) at angle of spread 10°	110°
Adult male	49	11.5	27.6	180.0
Juvenile male	43	11.6	27.8	181.6
Adult female	44	12.9	35.7	216.8
Juvenile female	45	12.9	35.6	215.5

TABLE 4. Flight surface area (wing plus tail at 110° angle of spread) and flight surface load (mass/flight surface area) of Merlins (*Falco columbarius*) captured at Cedar Grove, Wisconsin, during fall migration, 1978–1993.

	n	Flight surface (cm^2)	Flight load (g/cm^2)
Adult male	49	605.9	0.264
Juvenile male	43	622.8	0.247
Adult female	44	759.4	0.293
Juvenile female	45	753.4	0.282

wing loading was highly significant in both adults and juveniles, but the difference in aspect ratio was significant only in adults. Females had larger tail areas than males (Table 3). Females also had greater surface loadings than males (Table 4), but there were only slight differences between juveniles and adults.

Mueller et al. (1981) found that adult Sharp-shinned Hawks had significantly shorter tails, longer and wider wings, greater wing areas, higher wing loadings, and higher aspect ratios than juveniles. They hypothesized that adults flew faster and struck prey more forcibly, but required more energy consumption than juveniles. They proposed that juveniles were more maneuverable and required less energy in flight than adults and that this was an adaptation for the juveniles until they developed hunting skills for adult life. The pattern we found in Merlins is partially in agreement with this hypothesis. Adult males had greater wing loading and mass than juvenile males; however, the only significant age difference in females was in mass.

Sharp-shinned Hawks exhibit much greater age differences in aerodynamic characteristics than Merlins. Both species feed primarily on birds and have similar fledgling dependency periods (Sodhi et al. 1993, Bildstein and Meyer 2000). The major difference between the species is in how they hunt and capture birds. Sharp-shinned Hawks capture perched birds, often in dense vegetation, or in flight after a brief chase. Merlins usually capture birds in the air, often after a series of stoops at a flight speed considerably greater than that of Sharp-shinned Hawks. The tail and wings are used to deflect the airstream in rapid twists and turns. The force produced by such a deflecting surface is proportional to the area of the surface and the square of the airspeed, so a falcon in rapid flight needs less deflecting surface than a hawk in slower twists and turns. The tail of birds functions primarily as a control surface and a decrease in the ratio of mass to tail surface at maximum spread would increase maneuverability. This ratio in Sharp-shinned Hawks is only 58% of that of Merlins, suggesting that the former is considerably more maneuverable than the latter at equal airspeeds. The smaller age differences in wing width, wing length, and wing loading in Merlins, compared to Sharp-shinned Hawks, also can be attributed to Merlins not requiring relatively large control surfaces. Perhaps young Sharp-shinned Hawks need the additional maneuverability and economy in flight offered by lower flight loading, shorter wings, and longer tails, but these are of no advantage to young Merlins because speed is of prime importance in the pursuit of their prey.

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Social and Breeding Biology of Bee-eaters in Thailand

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ABSTRACT.—I report on the social and breeding biology of four bee-eater species in Thailand. Little Green Bee-eaters (*Merops orientalis*) breed cooperatively in clusters of overlapping territories. Cooperative breeding units have one to two helpers that join the breeding pair only after incubation has begun. Nests rarely are left unguarded due to threats of predation and possible intraspecific brood parasitism. Males also guard their mates against extrapair copulations. The Blue-tailed Bee-eater (*M. philippinus*) breeds cooperatively and has a complex social system, with evidence suggestive of intraspecific brood parasitism and extrapair copulation. I provide evidence that the Bay-headed Bee-eater (*M. leschenaulti*) breeds cooperatively and report observations of noncooperative breeding at one nest in the Blue-bearded Bee-eater (*Nyctyornis athertoni*).

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The bee-eaters (Aves: Meropidae) are a clade of 26 species with considerable diversity in social and breeding behaviors. This behavioral diversity includes colonial and solitary nesting, migratory and sedentary populations, and cooperative and noncooperative breeding systems. However, for several species data on these behaviors are lacking. These data are crucial for comparative studies concerning the evolution of, and the ecological influences on, bee-eater social system diversity. This paper describes aspects of the social structure and breeding biology of four bee-eater species breeding in Thailand.

The Little Green Bee-eater (*Merops orientalis*) is the most variable species in the family in regard to plumage color and can be subdivided into 6–8 geographically variable races (Fry 1984). Whether this species also shows variation in social and breeding behaviors in populations ranging from western sub-Saharan Africa through the Middle East and Indian subcontinent to south Asia is not known. To address this question, I compare the social system of Little Green Bee-eaters that were studied in Thailand and in India (Sridhar and Karanth 1993). Little information previously was available on the breeding biology of the Blue-tailed Bee-eater (*M. philippinus*), except that it sometimes nests in colonies (Fry et al. 1992). Here I show that this species breeds cooperatively and has a complex social system similar to other colonial bee-eaters. Lastly, I briefly describe the social system of the Bay-headed Bee-eater (*M. leschenaulti*) and the Blue-bearded Bee-eater (*Nyctyornis athertoni*).

METHODS

I made behavioral observations from 12 March through 5 May 1996. I studied Little Green Bee-eaters at Khao Sam Roi Yot National Park (99° 55′ E, 12°

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07′ N; Prachuap Khiri Khan Province; 110 h observation). The study area (0.23 ha) was an open deciduous woodland habitat immediately southwest of the park headquarters. Surrounding areas included open, dry marshlands, prawn farming ponds, mangrove-bordered streams, and open scrub. I studied Blue-tailed (59 h observation) and Bay-headed (11 h observation) bee-eaters on the banks of the Huai Sai Yai, approximately 15 km west-northwest of Ban Nadee (101° 37′ E, 14° 10′ N;, Prachinburi Province). Secondary growth deciduous forest and agricultural fields surrounded the river. I observed nesting Blue-bearded Bee-eaters in a montane evergreen rainforest at Khao Yai National Park (101° 35′ E, 14° 27′ N; Nakhon Ratchasima Province; 4.5 h observation).

I captured Little Green (n = 13) and Blue-tailed (n = 15) bee-eaters using mist nets and I marked individuals with unique combinations of nontoxic paints to allow recognition of individuals. I made behavioral observations of Blue-tailed Bee-eaters from within a blind. I estimated colony size in the Blue-tailed Bee-eaters by repeated censuses of the number of marked and unmarked individuals at the colony. I used the unbiased estimator Petersen method (Krebs 1989) to derive estimates of the colony size. This method estimates the colony size as

$$\hat{N} = \frac{(M + 1)(C + 1)}{R + 1} - 1,$$

where M is the number of individuals marked, C is the total number of individuals censused, and R is the number of marked individuals censused. I also calculated the 95% Poisson confidence limits for colony size (Krebs 1989). I collected 20 30-min focal individual observations of Little Green Bee-eaters from 5 to 10 April to quantify the time individuals showed nest guarding behavior. Nest guarding was identified as being inside the nest or perching ≤10 m and having an unobstructed view of the nest. Cavities at this time contained either completed or initiated clutches. I also recorded the frequency of perch changes, the behaviors associated with perch changes (e.g., flycatching, pursuit of predators, pursuit of conspecifics near nest), and the presence or absence of another bee-eater perched ≤10 m of the nest cavity. I also recorded other behaviors such as copulation and courtship feeding during focal observations. I considered individuals seen copulating and involved in courtship feedings as breeders. I considered individuals that did not copulate, showed submissive behaviors toward breeders (e.g., retreated when challenged for perch position), and brought food to nests as helpers. Species were considered to breed cooperatively if at least one nest had at least one helper. Means are reported with standard error values.

RESULTS

Little Green Bee-eaters.—Little Green Bee-eaters bred in clusters of overlapping home ranges. Breeders actively defended only the area immediately around their nest cavity (2–3 m). I found one cluster of seven nests dug into slightly sloped or flat ground. Mean distance between adjacent active nests in this cluster was 22.9 ± 6.2 m. Several additional unused nest holes were dispersed among those finally chosen for breeding. I found three additional active solitary nests just outside the main cluster of seven nests.

Breeding is quite synchronous among Little Green Bee-eater nests. Excavation of nest cavities was in its final stages or complete by mid-March. Courtship feedings (n = 44) and copulations (n = 14) were seen frequently during mid-March and early April. During five 30-min observation periods of one breeding pair during their laying period, courtship feedings (n = 24) and copulations (n = 7) were seen at a mean rate of 9.6 ± 3.4 and 2.8 ± 0.8 events/h, respectively. During 95% (42/44) of courtship feedings I witnessed, marked males fed only one marked female and marked females were fed by only a single marked male; however, in two groups I saw an extra individual feed the breeding female once. One group was feeding two fledglings on 3 May. On the same date, two nests contained nestlings near fledging age while two others had less developed nestlings. The remaining two nests on the main study area failed before fledging young.

One potential nest predator abundant in the area is the butterfly lizard (*Leiolepis belliana*). During 20 30-min observation periods, bee-eaters directed attacks composed of multiple dives at these lizards on five occasions (0.5 attacks/h). I saw 17 additional bouts of attacks at other times. This antipredator behavior also was directed less frequently toward dogs (n = 2) and a snake (n = 1). Scaly-breasted Munias (*Lonchura punctulata*) and a small, unidentified lizard species did not elicit this antipredator behavior, even when within 1–2 m of the nest. During the periods of egg laying and incubation, individuals spent a significant portion of their time in vegetation ≤10 m from their cavity that gave them clear views of the nest cavity (i.e., nest guarding behavior). I observed five individuals during 20 30-min observations to determine the frequency of this guarding behavior. Individuals spent a mean of 55 ± 8% of their time guarding the nest, with ≥2 individuals guarding 45 ± 8% of the time. Nests were left unguarded for only 18%

± 6% of the time. Males were much more active while guarding than were females, making a mean of 49.6 ± 8.8 perch changes/h versus 18.7 ± 6.2 for females. Most of these movements were associated with flycatching behavior (males: 36.0 ± 8.4 sallies/h; females: 9.3 ± 3.4).

Little Green Bee-eaters breed cooperatively in Thailand. Three or more individuals were associated with four of the seven nests (57%) on the main study site. At one additional nest, the breeding male disappeared during the study and I saw another individual shortly afterward bringing food to this nest. It is unclear whether this individual was a helper or a replacement mate. Two cooperatively breeding groups in the main study site and possibly another group observed on a single occasion outside the study site each contained two helpers. All other cooperative groups had a single helper. I saw helpers associated with breeding pairs only rarely before the onset of incubation. In fact, before egg laying was suspected to be complete, breeding males chased potential helpers from the area of both the nest and breeding female on 11 of 25 (44%) agonistic interactions seen. Eight of these eleven events involved a marked individual that subsequently did become a helper at this nest. The remaining three events involved unmarked individuals at three nests that subsequently also had unmarked helpers. The remaining 14 of 25 agonistic interactions (56%) involved neighboring breeders. Helper duties included mobbing predators, feeding nestlings, feeding fledglings, occasionally feeding the breeding female, and possibly incubation. Helpers contributed significantly to the quantity of food items brought to nestlings. At one nest, I observed the helper bring food items to the nest on seven of twelve occasions.

Blue-tailed Bee-eaters.—Blue-tailed Bee-eaters bred in a dense colony in a sandy riverbank. In the center of the colony, a 130-m^2 vertical area contained 49 nest cavities, 16–19 of which were active. The activity of three cavities was questionable because I saw individuals only perch in the cavity entrance on a few occasions. The remaining cavities were either nests from previous breeding seasons or false nests dug during the 1996 season. Eight additional active nests were located ≤20 m from the main colony. Three estimates of colony size were 38, 43, and 55 individuals (mean of 45.3) with lower and upper 95% Poisson confidence intervals ranging from 16.1–16.7 to 84.8–105.6, respectively.

Excavation of nests dominated colony activity during mid-March, but also occurred during late April at two nests. Birds at most nests made infrequent nest visits (mean of 0.65 ± 0.11 visits/h, 11 nests, 7.5 h observation), suggesting most individuals were incubating during late April. Two groups, however, were feeding nestlings during late April (mean of 2.25 ± 0.33 visits/h, 7.5 h observation). I found an egg in one female, a netting casualty on 27 April, during subsequent specimen preparation. Certain breeders therefore were unsynchronized by at least the length of the incubation period, a period of 19–21 days (Fry et al. 1992, P. F. Coulter and DBB unpubl. data).

Blue-tailed Bee-eaters breed cooperatively in Thailand. I observed at least three birds feed nestlings at eight nests. Helpers could have been present at other active nests and may have escaped detection due to the large number of unmarked individuals. Interactions among individuals in the colony were frequent and suggest a complex social system, similar to that of other colonial bee-eaters (Fry 1972, Emlen and Wrege 1986, Jones et al. 1991, Fry et al. 1992). Intraspecific brood parasitism may occur in this population. I saw three individuals enter at least two active nest cavities and five individuals perched at the entrance of either two or three active cavities each. Individuals vigilantly defended the immediate area around their nests by frequently displacing interloping individuals. Also, I found a cracked bee-eater egg with a small puncture on the ground outside a series of nest cavities from which it apparently had been ejected. These behaviors are consistent with those associated with confirmed brood parasitism in another population of Blue-tailed Bee-eaters (P. F. Coulter and DBB unpubl. data).

Bay-headed and Blue-bearded bee-eaters.—One Bay-headed Bee-eater nest was located on the edge of the Blue-tailed Bee-eater colony, while two others were located 45 m upstream. One nest was only 1 m from a Little Green Bee-eater nest. At least one nest had three individuals bringing food to nestlings during late April. These individuals repeatedly

perched outside the nest cavity, waiting in queue to feed nestlings.

I found a Blue-bearded Bee-eater nest along the orchid waterfall trail in Khao Yai National Park. The nest cavity was dug 1 m high in the side of a small pit. On 30 April, I observed two individuals frequently bringing food to nestlings. I saw no evidence of cooperative breeding at this nest.

DISCUSSION

In most respects the breeding biology of Little Green Bee-eaters in India (*M. o. orientalis*; Sridhar and Karanth 1993) and Thailand (*M. o. ferrugiceps*) were similar. In both areas the species bred cooperatively in small clusters of territories. In India 20–57% of groups had helpers over three years of study, with a mean of 38%. Cooperative breeding was found in four of seven groups in Thailand. In India only a single helper was seen in attendance at each cooperative nest, while in this study two helpers were seen in two of four cooperative groups.

Helpers typically arrived after the start of incubation. Indeed, in this study the behavior of breeding males at early stages of breeding indicated that helpers may have been a threat with regard to extrapair copulation and/or intraspecific brood parasitism. Extrapair individuals that brought food to or simply perched near breeding females were displaced by breeding males, as were individuals who approached the nest cavity.

Two alloparental duties provided by helpers in many cooperative breeding species include feeding young and protecting young from predators (Brown 1987). Helpers in this study delivered a substantial portion of the food items to nestlings, as was the case in India. Little Green Bee-eaters also spent a substantial portion of their time guarding their nests. Frequent diving attacks were directed toward butterfly lizards and other potential predators when they approached the area of the nest cavity. In India, nests with helpers (n = 9) experienced no predation, while those without (n = 15) suffered 20% predation (Sridhar and Karanth 1993).

Previously, very little information was available on the remaining species studied here. Blue-tailed Bee-eaters were known to nest both solitarily and colonially, with colonies commonly containing 10–30 active nests and occasionally up to hundreds (Fry et al. 1992). The colony studied here was a small colony. This study is the first to document that Blue-tailed Bee-eaters breed cooperatively. This species shows additional similarities to other colonial cooperative breeding bee-eaters: Red-throated (*M. bullocki*), White-fronted (*M. bullockoides*), and European (*M. apiaster*) bee-eaters. Interactions among colonial individuals both within their own and among different breeding groups can be complex and lead to variable patterns of maternity and paternity associated with each nest (Fry 1972, Emlen and Wrege 1986, Jones et al. 1991, Fry et al. 1992). Molecular studies show that behavioral observations alone can lead to large underestimates of the effective rate of extrapair copulations and brood parasitism (Wrege and Emlen 1987). If any evidence of these behaviors exists, then they may be quite common. The behaviors seen in this study are strongly suggestive that extrapair copulation and intraspecific brood parasitism occur in Blue-tailed Bee-eaters.

Concerning the Bay-headed Bee-eater, an unpublished study cited by Sridhar and Karanth (1993) claims that cooperative breeding occurs in India. Blue-bearded Bee-eaters apparently breed only in solitary pairs (Fry 1984, Fry et al. 1992). Observations described here support those conclusions.

It is likely that at least 15 of the 26 species of bee-eaters breed cooperatively (Burt 1996). Some species, such as the Little Green Bee-eater, show slight geographic variation in breeding behavior. As the basic behavioral and natural history data are documented for all bee-eaters, phylogenetically explicit comparative studies will be possible and will lead to an understanding of the patterns of behavioral evolution in this group and the ecological forces that have molded these patterns.

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Genetic Evidence for Extrapair Paternity in the Tufted Titmouse

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ABSTRACT.—Until now, there have been no reports of extrapair parentage in Tufted Titmice (*Baeolophus bicolor*). During 1995–1998, we used multilocus minisatellite DNA fingerprinting to estimate paternity and degree of relatedness in eight central Ohio broods of this socially monogamous species. Our results suggest a rather low rate of extrapair fertilization in the study population; three of 34 nestlings could not be attributed to the attending male. Of the three extrapair offspring, two represented the entire brood in a nest attended by their mother and a nonparental male that appeared to be a close relative of the mother.
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During recent years, molecular techniques have revealed instances of extrapair parentage in socially monogamous birds (e.g., Parker and Burley 1998). Extrapair copulations are a strategy by which individuals can increase their reproductive success. Known rates of extrapair paternity in avian species vary from 0–85% (Gowaty 1996). Because social monogamy and biparental care are typical of passerines, this group is well represented in studies of genetic similarity within broods.

The Tufted Titmouse (*Baeolophus bicolor*) is a permanent resident, socially monogamous, cavity-nesting passerine common in the eastern deciduous woodlands of North America (Grubb and Pravosudov 1994). We used DNA fingerprinting to assess extrapair parentage in central Ohio broods of Tufted Titmice. Until now, there have been no reports of extrapair behavior in Tufted Titmice. In our study area within a suburban landscape, titmice breed in Eastern Bluebird (*Sialia sialis*) nest boxes in edge habitat near small forest fragments and golf courses. Since titmice seem to prefer natural cavities over nest boxes, and since availability of trees with cavities

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is low in suburban habitat, their breeding density in our study area is considered low even in places where nest box availability is high (D. Sillick and R. Tuttle pers. comm.). In addition, the natural cavities used by titmice as nesting sites are almost always located in very large deciduous trees high above the ground and are difficult to access, which explains scarcity of data on breeding biology of this common species (Grubb and Pravosudov 1994). Thus, we feel that any new data concerning Tufted Titmouse reproductive biology are extremely valuable.

We studied nine broods of Tufted Titmice from nest boxes in suburban Franklin and Delaware counties, Ohio (40° 00′ N, 82° 53′ W) during May and June, 1995–1998. Mean brood size was 4.2 ± 1.1 SD nestlings. We mist netted adults at the nests when nestlings were 5–10 days old. Adults and nestlings were fitted with USFWS aluminum bands, and adults also with plastic color bands. Sex of adults was determined using size dimorphism and presence of brood patch (Pravosudov et al. 1999). On the day adults were captured, a 50-μl blood sample was taken from the brachial vein of each nestling and attending adult, shaken with 500 μl of lysis buffer (100 mM Tris, pH = 8.0, 100 mM EDTA, 10 mM NaCl, 5% SDS; Longmire et al. 1988), and stored at ambient temperature. All families represented first nesting attempts of the season. Although some nest boxes were occupied twice during consecutive years, all adults were used only once. At one of the nests, we captured the attending female, but failed to catch the male, so this brood had to be excluded from analysis of paternity. However, since our primary concern was to determine paternity rates, and since intraspecific brood parasitism has not been reported in parids (Kempenaers et al. 1995), we included one family where only the attending male was captured. To estimate parentage we used multilocus minisatellite DNA fingerprinting (Jeffreys 1985a, 1985b). Procedure is described in detail in Pravosudova et al. (1999). Individual samples from the same family were positioned next to each other on a gel, and the degree of band sharing (x) between individuals (Wetton et al. 1987) was calculated. The number of novel bands (i.e., bands not found in either of the putative parents) in the profile of each nestling was counted.

An attending adult was not excluded as a parent of a particular nestling if the band-sharing value between the two birds was high (>0.46) and the number of novel bands in the profile of the nestling did not exceed two. In cases where parentage could not be confirmed otherwise, the band-sharing value of 0.46 was used as a conservative threshold for assigning first order relatives (for details see Pravosudova and Grubb 2000: fig. 1). Using the mean proportion of bands shared between presumably unrelated individuals (x = 0.28), we calculated the probability of mistakenly assigning an unrelated bird as a parent (Rabenold et al. 1991) as 1.2×10^{-4}.

A mean of 21.07 ± 3.30 SD bands were scored per lane, with dyadic band-sharing values ranging from x = 0.18 to x = 0.92. In seven of the broods, 26 of 29 nestlings could be attributed to both attending adults. The number of novel bands in the profiles of these 26 young, apparently related to both attending adults, ranged from 0–2 (mean = 0.65 ± 0.74 SD, n = 26). In the eighth brood, where the male was the only adult attending the nest, band-sharing values between each of the five nestlings and him was above the 0.46 threshold (x = 0.53 ± 0.05 SD, n = 5).

Three of the nestlings could not be assigned to the attending male (mean number of novel bands was 5.00 ± 1.00 SD, n = 3). One of these nestlings apparently was a "true" extrapair offspring (band sharing with putative father: x = 0.35, 5 novel bands) in a nest with three other young, all of which were highly related to both members of the territorial pair. The remaining two unattributed nestlings were the only chicks in a nest attended by their mother and a nonparental male. While the band-sharing values between this attending male and the nestlings were quite high (x = 0.41 and x = 0.49), the comparatively large number of unattributable bands (4 and 6) in the profiles of the young made us exclude him as the genetic father. Band-sharing analysis (x = 0.53) suggested that the attending male could be a first order relative of the attending female. Taking into account all the unattributed nestlings, the conservative estimate of extrapair fertilizations rate, 8.8% (estimated 95% confidence interval: 0–18.7%), is still

relatively low. Reported EPP rates for other parids range from 0.9% in Willow Tits (*Parus montanus*; Orell et al. 1997) to 25.3% in Coal Tits (*P. ater*; Lubjuhn et al. 1999). Variation also exists among populations of the same parid species. For example, in Great Tits (*P. major*), EPP rates from 3.5% (Verboven and Mateman 1997) to 15% (Gullberg et al. 1992) have been reported.

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Ornithological Literature

Edited by Sara R. Morris

BEHAVIORAL ECOLOGY OF TROPICAL BIRDS. By B. J. M. Stutchbury and E. S. Morton. Academic Press, New York. 2001: 165 + ix pages, 31 black-and-white figures. $69.95 (cloth), $39.95 (paper).—The authors' intent in writing this book was to demonstrate the differences between tropical birds and those that reside in or migrate to temperate zones to breed, especially to ornithologists and behavioral ecologists steeped in the lore of Temperate Zone dogma. They postulate that too many of the underlying assumptions of the developing field of behavioral ecology are based on temperate models. Do tropically breeding birds differ from their temperate counterparts? They do in many ways. The authors use these differences to examine and test several general hypotheses in behavioral ecology. The answers they propose often not only provide explanations for the evolution of behavioral and morphological traits found in tropical species, but also offer plausible and testable explanations for temperate breeding species. A recurring theme throughout the book is that "empirical data and field experiments are severely needed" to distinguish between hypotheses that are valid only for temperate species and those that are general. For example, extrapair fertilizations appear to be common in Nearctic monogamous passerines but extremely rare in Neotropical monogamous passerines. Because of the longer breeding season and greater asynchrony among females in the tropics, there would be more opportunities for extrapair copulations in tropical species. What are we missing?

The authors pose this book as a "call to arms" for behavioral ecologists to investigate tropical species to generate models that are more general and less limited by constraints of the Temperate Zone before it is too late; many of these species occupy habitats that are being degraded rapidly by human activity. The effects of the loss of large tracts of habitat are obvious: the physical structures needed by the birds for survival are removed. Less obvious are the effects of selective logging (often posed as an alternative to clear-cutting) and the establishment of a road or even a trail. Some species, such as the Guianan Cock-of-the-Rock (*Lepidothrix serena*), the White-throated Manakin (*Corapipo gutturalis*), and the White-fronted Manakin (*L. serena*), require the intermix of sun and shade that produces sunflecks for their courtship arenas. These birds display with their bodies partly in full sun and partly in the shade. Removal of single trees from the wrong locations would open up the sites to full sun and eliminate breeding from the areas.

Although short, only 130 pages of text, the book raises many thought-provoking questions. I highly recommend it for anyone interested in tropical ornithology or behavioral ecology. For those interested only in Temperate Zone patterns of behavioral ecology, it should be mandatory reading. The book is well written and as easy to read by those not versed in the jargon of the field as it is by researchers of behavioral ecology.—ROBERT C. BEASON.

BIRDS OF THE TEXAS PANHANDLE. By Kenneth D. Seyffert, illustrated by Carolyn Stallwitz. Texas A&M Univ. Press, College Station, Texas. 2001: 501 pp., 10 black-and-white illustrations, 1 map, species checklist by county. $49.95 (cloth), $24.95 (paper).—Although at first the geographic coverage of this book might seem limited, the author extends his coverage to include the adjacent counties of New Mexico and Oklahoma. Thus, the resulting area is larger than some states, with elevations extending to almost 1,500 m. Along with the elevational variation are variations in habitat that have resulted in 442 species reported for the region and 151 confirmed breeding species. In the introduction, the author gives an overview of the region and describes the more important birding locations in some detail, indicating which species can be found in each location.

I commend the author for adopting the abundance-residence terminology used in the *Birds of North America* series. It seems that many authors want to invent their own categories rather than using one that is somewhat standardized. The species accounts contain information on status, occurrence, nesting, and specimens. The data on occurrence is the most extensive, including information on when and in which counties the species has been observed, in which of the important birding areas it occurs, and often the average numbers seen by county on Christmas Bird Counts and Breeding Bird Surveys. The reading of the text would have been improved if the census data were summarized and the numbers put into an appendix table instead of stuck within the text descriptions.

For many species accounts the "Occurrence" and "Nesting" sections contain published and unpublished (the author's own) anecdotes of the species. Thus, the book is a blend of metrics (dates, numbers, and counties) and anecdotal snippets. This approach probably was taken to appeal to casual birders as well as those seeking details about change in chronology or abundance of a species. The result is text that is not well integrated. The length of the species accounts differ greatly. As might be expected, breeding accounts for common species tend to be larger than accounts of rare transients, but even some of the latter are lengthy. The length appears to depend upon the author's interest in or interaction with the particular species. The appendix contains a species checklist (presence only) by county. As the author points out, the lack of a record for many species for some of the counties results from the lack of observers, not necessarily the absence of the species. The counties near Amarillo and the other cities have received the greatest coverage.

Illustrations are limited to 10 attractive pencil drawings and a cover watercolor by Carolyn Stallwitz. The book will be most valuable to individuals working in the Texas-Oklahoma panhandle area. For those individuals, the book will serve as a valuable reference on the distribution and abundance of avian species. The extensive bibliography provides references to the literature examined by the author and will be a good resource for others working in this region.—ROBERT C. BEASON.

BIRDS OF THE SOUTHWEST. By John H. Rappole. Texas A&M Univ. Press, College Station, Texas. 2000: 329 pp., 457 color photographs, 457 range maps, 45 numbered figures. $36.95 (cloth), $17.95 (paper).—The area covered by the book is New Mexico, Arizona, southern California, and the southern tip of Nevada. This is neither a field guide nor an exhaustive distributional analysis. There is a color photograph, range map, and species description for each of 457 species. The quality of the color photographs generally is good to excellent. Most of the birds were photographed in breeding plumage, but there are some cases of winter plumages. One error that slipped past proofing is that after species number 246 (Northern Flicker, *Colaptes auratus*), the picture numbers no longer coincide with the numbers on the species accounts. The range maps denote the distribution and seasons of occurrence, but they are small and provide no detail. Each species account is brief, half a page or less. The accounts contain information on general description, vocalizations, similar species, habitat, abundance, distribution, where to find (in the Southwest), and range (in North America). Another error that got past proofing is that some of the locations listed for a species in the "Where to Find" section are outside the species' distribution given in the range map.

The introduction contains material on landforms, climate, and habitat. These sections should be especially useful to those not familiar with the Southwest. The section "Using this Guide" ends with an admonition on preparing for a birding trip to remote areas of the Southwest. For those who live or have lived there, the precautions are obvious and automatic. To residents of more moist and benign climates, this advise needs to be followed; a bit of common sense and safety precautions interjected into a birding guide. The last section of the book is a list of birding sites by state, with detailed instruction on how to get to each site and which species one can expect to see. This list includes many of the locations I have frequented and some with which I am

not familiar. There also are several popular birding locations that are not listed. Overall, it is a good starting list for someone new to the area.

This book will be useful to anyone wanting to visit the region, especially those who are unfamiliar with it. The advantage of this volume is that it summarizes the information of several more exhaustive, but geographically restricted, guides for the Southwest. I highly recommend the book as a single volume for people traveling to the Southwest to bird.—ROBERT C. BEASON.

HANDBOOK OF THE BIRDS OF THE WORLD, VOLUME 7: JACAMARS TO WOODPECKERS. Edited by Joseph del Hoyo, Andrew Elliott, and Jordi Sargatal. Lynx Editions, Barcelona, Spain. 2002: 613 pp., 49 color plates and numerous color photographs. $185 (cloth).—This book covers the Galbuliformes and the Piciformes, thus completing the coverage of the nonpasserines in the *Handbook of the birds of the world.* The forward to this book, written by Errol Fuller, is an extensive discussion of extinct birds. The 58-page forward includes a general introduction to rarity, reasons for extinction, and hypothetical species, those that are known from only a single specimen or from a description. Brief descriptions of extinct species follow the general introduction and cover 72 species that are generally recognized as extinct. These accounts include the well-known cases of the Great Auk (*Pinguinus impennis*), Dodo (*Raphus cucullatus*), and Carolina Parakeet (*Conuropsis carolinensis*), but also cover many less-well-known species, including a disturbing number of birds that were endemic to various islands and island archipelagos. The attention to detail in the forward is demonstrated by the extensive list of references, which covers five pages.

The organization of the text is similar to previous volumes. The family accounts begin with a range map and general description of members of the family. The text that follows this introduction is organized into sections on systematics, morphological aspects, habitat, general habits, voice, food and feeding, breeding, movements, relationship with man, status and conservation, and a general bibliography. The text is accompanied by numerous well-chosen photographs of family members. Following the text on each family are individual species accounts that provide taxonomic information including the scientific name and names in French, Spanish, and German; information on the original description; and information about superspecies, subspecies, and races. A description of the family's distribution is accompanied by a range map. Additional sections within the individual accounts cover descriptive notes, habitat, food and feeding, breeding, movements, status and conservation, and a bibliography. J. A. Tobias authored the section on the jacamars (Galbulidae) and coauthored the species accounts for this family with T. Zchner and T. A. de Melo-Júnior. The section on the Bucconidae (puffbirds) was authored by P. C. Rasmussen and N. J. Collar. L. L. Short and J. F. M. Horne coauthored three of the four family accounts within the Piciformes, which cover the Capitonidae (barbets), the Ramphastidae (toucans), and the Indicatoridae (honeyguides). The section covering the Picidae (woodpeckers) was written by H. Winkler and D. A. Christie.

A laminated index to the first seven volumes of the *Handbook of the birds of the world* is included with volume 7. One side is organized systematically and includes illustrations of a representative member of each family as well as the volume and page number for the family description. The other side of the index is in alphabetical order and includes orders, families, and general common names.

In the introduction to volume 7, the editors discuss the results of a poll in which they asked readers whether they preferred "the recent trend of longer, fuller texts, more photos, and more extensive coverage of subspecific variation on more plates." An overwhelming 93% of the almost 3,000 respondents preferred the expanded coverage, even if it resulted in more than the originally estimated 12 volumes in this series. The editors have made a wise decision to continue their expanded coverage and make this indispensable reference even more useful to ornithologists. As with previous volumes in this series, this volume is a must in any ornithological library.—SARA R. MORRIS.

THE SIBLEY GUIDE TO BIRD LIFE AND BEHAVIOR. Edited by Chris Elphick, John B. Dunning, Jr., and David Allen Sibley; illustrated by David Allen Sibley. Alfred A. Knopf, New York. 2001: 608 pp., numerous color figures and maps. $45 (cloth).—The *Sibley guide to bird life and bird behavior* is an interesting reference that combines much general information about basic bird biology and the birds of North America. The book is organized into two major parts: (1) the world of birds, and (2) bird families of North America. The introduction, glossary, checklist, and index provide additional resources for the reader.

The introduction is well prepared, not only providing information about how and why the editors chose certain organization and conventions, but also providing substantial references for additional information about birds and bird biology. The introduction includes the sections "How the book is organized," "Bird names and classification," "Sources of information," "Worldwide family features," "Conservation," and "Acknowledgments."

Part I, "The world of birds," begins with "Flight, form, and function," which includes sections of the implications of flight; the structure and types of feathers; molts and plumage; aerodynamics; feet, bills, and digestion; bones and muscle; respiration and metabolism; senses and vocal apparatus; and bird intelligence. "Origins, evolution, and classification" includes information on the origin of birds; the "trees-down" and "ground-up" theories of the origins of flight; how bird species originate; classification, including schemes and methods of classification; and species concepts. "Behavior" includes information of the study of bird behavior; the function of bird behavior; daily and seasonal rhythms, including the control and coordination of seasonal activity; daily maintenance behaviors, including feeding, feather care, locomotion, and concealment; migration; dispersal; communication; reproductive behavior; and understanding behavior. The section on reproductive behavior includes information on mating systems, territoriality, coloniality, cooperative breeding, brood parasitism, and parental care. "Habitats and distributions" includes introductory material on range and habitat and habitat distribution patterns followed by sections on the individual habitat types of forests and woodlands, grasslands, shrublands, deserts, tundra, wetland and aquatic habitats, ocean habitats, and human created habitats. Part I ends with "Populations and conservation" that includes a discussion of what determines bird population sizes, population regulation, conservation threats, tracking bird population in North America, and protecting North American birds.

Part II covers the families of birds of North America. The family accounts generally include sections on taxonomy, habitats, foraging, breeding, conservation, and a summary of the key information about the family worldwide. However, accounts of individual families often also include additional information pertinent to that family. For example, the account covering plovers and lapwings (Charadriidae) includes additional sections on variation and molt, habitats, and movements, and the account covering tyrant flycatchers (Tyrannidae) includes additional sections on variation, habitats, adaptations to lifestyle, and migration. Some less common families, e.g., thick-knees (Burhinidae) and hoopoe (Upupidae), are given only minimal coverage, but are included because one or more species has been seen in North America.

Although one might argue that additional space could have been dedicated to many of the individual sections or that some of the sections would benefit from a different organization, overall the coverage and the organization are effective.

The *Sibley guide to bird life and bird behavior* is an excellent source of easily accessible, general information about birds for most bird enthusiasts. Although this book is unlikely to replace Gill's *Ornithology, 2nd ed.* (1995, W. H. Freeman, New York) as a text for traditional ornithology courses, it provides a possible alternative text for bird biology courses for nonmajors or for noncredit courses.—SARA R. MORRIS.

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NEST AND EGGS OF THE TEPUI ANTPITTA (*MYRMOTHERA SIMPLEX*)

BRIAN R. BARBER[1,2] AND MARK B. ROBBINS[1,3]

ABSTRACT.—We describe for the first time the nest and eggs of the Tepui (Brown-breasted) Antpitta (*Myrmothera simplex*). Nest structure and eggs are very similar to those described for *M. simplex*'s extant sister species, the Thrush-like Antpitta (*M. campanisona*), and nests of this genus are similar to those described for other members of the ground antbirds (Formicariidae). *Received 23 October 2001, accepted 28 June 2002.*

On 24 March 2001, while conducting an avifaunal inventory of the north slope of Mount Roraima, Guyana (05° 17′ N, 60° 45′ W), we flushed and collected a female Tepui Antpitta (*Myrmothera simplex*; KUNHM 92366) from near the ground at 700 m elevation. Shortly after recovering her, we located a nest with two eggs a few meters away in a relatively flat section of an otherwise steeply sloped region of extensive undisturbed forest. Upon discovering the nest at 09:55 EST, BRB immediately began observations while MBR retrieved a camera. At 09:58, a presumed adult male antpitta flew to the rim of the nest and began incubation. Aside from occasionally moving his head from side to side, he remained motionless until 10:45 when he stood up and appeared to shift at least one of the eggs with his beak. Incubation continued until 10:55 when he was flushed from the nest. The following day he was collected (testes 7 × 4 mm; USNM 622748) by C. Milensky. This represents the first time both sexes of *Myrmothera* have been observed incubating, but this behavior has been documented for other formicariid genera (Wiedenfeld 1982).

The solid, cup-shaped nest was about 0.6 m above the ground placed among the leaf bases and petioles of *Philodendron linnaei* Kunth (Araceae; Frontispiece). The nest was comprised primarily of small sticks with dead leaves at the base. The cup was lined with smaller sticks and rootlets. Nest dimensions were as follows: inside diameter ca 101 × 90 mm, inside depth 56 mm, height 145 mm. The eggs were oval with a light blue ground color (similar to, but paler than that of the American Robin, *Turdus migratorius*) with sepia colored spots primarily at the larger end. Dimensions of the two eggs were 26 × 20 mm and 27 × 20 mm (KUNHM 92366). The following data

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←

FRONTISPIECE. Nest and eggs of the Tepui (Brown-breasted) Antpitta (*Myrmothera simplex*), north slope of Mount Roraima (700 m), Guyana, 24 March 2001. Photograph by M. B. Robbins.

were recorded when the female was prepared: ovary mass 7 × 5 mm, oviduct 3 mm in diameter and convoluted, body mass 46.8 g, light fat.

The nest and eggs of *M. simplex* are very similar to those described for its closest living relative, *M. campanisona* (Tostain and Dujardin 1988). In fact, the nest and the color and dimensions of the eggs described for *campanisona* are so similar to those of *simplex* that we suspect that they would be very difficult to distinguish. However, the two species are separated elevationally where their geographic distributions overlap. On the north slope of Roraima we found *campanisona* no higher than 500 m, whereas *simplex* was not encountered below 700 m. In the absence of *simplex*, we have found *campanisona* ranging as high as 1,000 m in the Acari Mountains of southern Guyana, and in the Andes *campanisona* has been recorded as high as 1,200 m (Ridgely and Tudor 1994). *Myrmothera* nest structure and placement is most similar to the larger, more terrestrial formicariids in having a bulky platform nest constructed of dry coarse leaves, twigs, and/or petioles and located atop trunks or in palm or aroid leaves (Skutch 1969, Wiedenfeld 1982, Protomastro 2000). In contrast, nests of the smaller, more arboreal *Grallaricula* are constructed primarily of fresh, green moss and located in forks of small saplings and vines (Holley et al. 2001).

There appears to be a fair amount of variability in egg color among the ground antpitta assemblage. However, congeneric differences are slight; the following summary is from Schönwetter (1979), Wiedenfeld (1982), Whitney (1992), and Holley et al. (2001): *Hylopezus* (light gray, pale olive buff, or yellowish brown), *Grallaria* and *Myrmothera* (greens and blues with dark blotches), *Grallaricula* (light coffee brown with dark blotches), and *Formicarius* and *Chamaeza* (white).

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We thank D. Nicolson, D. Clarke, V. Funk, and T. Hollowell for plant identification. N. Holcroft provided English translations of the German literature. Our work was part of a long term assessment of the avifauna of Guyana by the bird divisions of the Univ. of Kansas Natural History Museum (KUMNH), the National Museum of Natural History (USNM; Smithsonian Institution), and the Univ. of Guyana under the auspices of the Biological Diversity of the Guianas Program. This is number 53 in the Smithsonian's Biological Diversity of the Guianas Program publication series. The Guyana Environmental Protection Agency kindly granted field work and collecting permits. Partial funding of BRB's participation was through the generosity of the Rudkin Award for Undergraduate Research at the Univ. of Kansas and the Burroughs Audubon Society. MBR's involvement was made possible through a grant from the Blake Fund of the Nuttall Ornithological Club and a National Geographic Society grant to him and M. Braun.

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FIRST REPORT OF A GROUND NEST OF CANYON TOWHEES

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ABSTRACT.—Canyon Towhees (*Pipilo fuscus*) normally nest in trees, shrubs, and cacti. I found a nest on the ground under an octagonal road sign in Santa Fe County, New Mexico, on 14 May 2001. No young were fledged, but the eggs were incubated for ≥10 days. Additional records of Canyon Towhee nests in a building and an enclosed trailer are indicative of a plasticity in their nest site selection process that led to use of this unusual nest site. *Received 16 January 2002, accepted 22 August 2002.*

Recent check-list revisions have brought the genus *Pipilo* back up to eight species, all found between southern Canada and southern Mexico (American Ornithologists' Union 1998). At least three of the four more brightly feathered towhees commonly nest on the ground (i.e., Greenlaw 1996), usually within dense brush or scrub. Of the four species of drab "brown" towhees that occupy more open habitats, only the California Towhee (*P. crissalis*) has been recorded ground nesting, and only two instances are known (Davis 1951). Canyon Towhees (*Pipilo fuscus*) typically build their nests 1–4 m above the ground in trees, shrubs, or cacti (Johnson and Haight 1996). At its northern range limits and at higher elevations in Colorado and New Mexico, this species regularly nests in pinyon pine (*Pinus edulis*), juniper (*Juniperus* spp.), sagebrush (*Artemesia tridentata*), and cholla cactus (*Opuntia* spp.; Johnson and Haight 1996). The lowest previously reported nest was 0.6 m above ground in a small, 0.75-m high cholla in Tucson, Arizona (Brandt 1951). Here I report the first known instance of ground nesting by Canyon Towhees.

At 12:15 MST on 14 May 2001, while walking in Eldorado, a residential subdivision in Santa Fe County, New Mexico (35° 33′ N, 105° 57′ W), I accidently flushed a drab towhee-sized bird from under a decumbent 50-cm diameter octagonal "STOP" sign. Lifting the sign, I found three eggs, whitish with brown spotting, in a nest cup of herbaceous twigs and grasses nestled amidst the vegetation (Fig. 1). The closest tree or bush was >10 m distant. I returned on 15 May, confirmed the identity of the flushing adult as a Canyon Towhee, and photographed the nest.

On my next visit, at 18:10 on 17 May, I found the sign had been turned over to one side, exposing the nest. It was still intact and contained the three eggs. I returned the sign to its position over the nest. I again flushed the female from the eggs on 24 May. However, on 7 June, the nest was disheveled and contained only half an eggshell, which was yolk-stained. Although the sign was still over the nest, an area of approximately 25 m^2 next to the sign recently had been mechanically mowed. It was not clear whether nest failure was the result of predation or human interference.

Canyon Towhees are found near outbuildings, woodpiles, and vehicles throughout their range (Johnson and Haight 1996) and are common in Eldorado, which is characterized by 0.4- to 1.0-ha lots and mostly native vegetation. This association with structures is not accompanied by numerous records of nesting in them; Johnson and Haight (1996) reported only two nests in buildings, including one in Santa Fe County (see Jensen 1923). During 12 years of recent residence at two locations in Santa Fe County, I have documented Canyon Towhees nesting in man-made structures on seven occasions. Three were in a building, three were in an enclosed horse trailer, and one was in a nest box with an enlarged entrance. I believe this willingness of Canyon Towhees to use man-made structures as nest sites led to the use of this ground nest hidden by the sign.

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FIG. 1. Ground nest and eggs (metal sign post on left) of Canyon Towhees, Santa Fe County, New Mexico, 15 May 2001. Photograph by D. W. Stahlecker.

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ARE PILEATED WOODPECKERS ATTRACTED TO RED-COCKADED WOODPECKER CAVITY TREES?

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ABSTRACT.—Pileated Woodpeckers (*Dryocopus pileatus*) cause damage to Red-cockaded Woodpecker (*Picoides borealis*) cavity trees in the form of cavity enlargement or other excavations on the surface of the pine tree. However, it is not known whether Pileated Woodpeckers excavate more frequently on Red-cockaded Woodpecker cavity trees than on noncavity trees or how stand structure is related to the frequency of Pileated Woodpecker excavation. Also, it is unclear whether the cavity itself provides the stimulus to Pileated Woodpeckers to excavate or whether the presence of Red-cockaded Woodpeckers and their activities are attracting them. We surveyed all of the Red-cockaded Woodpecker cavity trees (n = 202) and 110 control trees in the loblolly (*Pinus taeda*)-shortleaf (*P. echinata*) pine habitat on the Angelina National Forest for recent Pileated Woodpecker excavation and found that approximately 7.4% of all cavity trees were damaged while no control trees showed any evidence of Pileated Woodpecker damage. The rate of Pileated Woodpecker excavation was negatively associated with hardwood midstory height and density. Pileated Woodpeckers appeared to focus most of their excavations on Red-cockaded Woodpeckers cavity entrances. We suggest that Pileated Woodpeckers may be attracted to Red-cockaded Woodpecker cavity trees, especially the cavity, and that midstory removal used to improve Red-cockaded Woodpecker habitat may increase the incidence of damage to the cavity trees by Pileated Woodpeckers in the current fragmented landscape. *Received 24 January 2002, accepted 12 August 2002.*

The endangered Red-cockaded Woodpecker (*Picoides borealis*) evolved in the fire-maintained upland pine savannahs of the southeastern United States (Jackson 1971, Conner et al. 2001). This species may have gained an evolutionary advantage by excavating its roost and nest cavities almost exclusively in living pine trees (Ligon 1970), thereby becoming the most common woodpecker species in an environment where snags likely were short lived due to frequent fires.

Excavating a roost or nest cavity in a living pine tree is a slow process for Red-cockaded Woodpeckers, often taking 2–6 years of intermittent excavation to complete (Conner and Rudolph 1995). A group of Red-cockaded Woodpeckers, usually composed of a breeding pair and one to three helpers (Ligon 1970, Lennartz et al. 1987), excavate roost and nest cavities and defend them from conspecifics. The aggregation of cavity trees excavated by a group of birds is termed the cavity tree cluster. Red-cockaded Woodpeckers excavate shallow holes, termed resin wells, through the bark to the cambium on active trees (cavity trees currently used for roosting or nesting). Resin well excavation likely evolved as a method to keep the cavity entrance open in the living tree (Conner et al. 2001). Left undisturbed, the cambium layer grows over the cavity sealing the entrance (DS and RNC pers. obs.). As a consequence of the frequent resin well pecking, copious amounts of resin flow down the bole of active cavity trees and serve as a barrier to rat snakes (*Elaphe* spp.; Jackson 1974, Rudolph et al. 1990) and occasionally other wildlife species (Schaefer and Saenz 1998). In addition to active cavity trees within the cluster, there often are other inactive cavity trees used previously by woodpecker group members. Cavity tree clusters also can be categorized as active or inactive, with active clusters having at least one active cavity tree. Inactive clusters are sites that have been abandoned by the woodpeckers.

Pileated Woodpeckers (*Dryocopus pileatus*) enlarge Red-cockaded Woodpecker cavities, thereby making them unsuitable for Red-cockaded Woodpeckers, and damage cavity trees (Conner and Rudolph 1995, Saenz et al. 1998). However, Pileated Woodpeckers rarely use enlarged cavities as roost or nest sites (Conner et al. 1997a). It is not clear why Pileated Woodpeckers damage Red-cockaded Woodpecker cavity trees, or if they select them over noncavity trees in the forest. However, Pileated Woodpeckers can destroy cavi-

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ties faster than Red-cockaded Woodpeckers can excavate them (Conner and Rudolph 1995), which could contribute to the decline of this endangered species. Techniques such as artificial cavities (Copeyon 1990, Allen 1991) and restrictors (Carter et al. 1989) have been developed to provide new cavities and protect existing ones.

Our primary objective was to determine if Pileated Woodpeckers are attracted to Red-cockaded Woodpeckers cavity trees. Secondarily, we wanted to identify any characteristics of cavity trees or the cavity tree cluster, such as midstory condition or the presence or absence of Red-cockaded Woodpeckers, that might make cavity trees more or less attractive to Pileated Woodpecker for excavation. Finally, we discuss the potential effects of landscape level events, such as fire suppression and forest fragmentation, which could have increased the co-occurrence and interactions of these two woodpecker species.

STUDY AREA AND METHODS

We studied the interaction between Pileated and Red-cockaded woodpeckers on the Angelina National Forest (31° 15′ N, 94° 15′ W) in eastern Texas. This forest is characterized by having two distinct pine habitat types. The northern portion of the forest is dominated by loblolly (*Pinus taeda*) and shortleaf (*P. echinata*) pine in the overstory, whereas the southern portion of the forest is composed predominantly of longleaf pine (*P. palustris*) in the overstory where Red-cockaded Woodpeckers occur. Most of the cavity tree clusters in both portions of the forest contained naturally excavated cavities and artificial cavities. Almost all of the artificial cavities in the Angelina National Forest are the "insert" type developed by Allen (1991). In general, all the cavity tree clusters were managed to provide adequate Red-cockaded Woodpecker habitat, although active cavity tree clusters received priority management, particularly hardwood midstory reduction and suppression, over inactive clusters.

We examined Pileated Woodpecker damage to Red-cockaded Woodpecker cavity trees between 15 March 2000 and 15 April 2000. We examined all Red-cockaded Woodpecker cavity trees for signs of recent (within 2–3 months) cavity enlargement or Pileated Woodpecker damage on the boles of the trees. We distinguished recent excavations from old by their bright yellowish appearance. By using only recent excavations for our comparisons we were able to control for the length of time a cavity has been in existence. For example, a cavity that has been in existence for several years may have a higher probability of having some Pileated Woodpecker damage during its existence than a newer cavity.

To address our primary objective we compared the incidence of recent Pileated Woodpecker excavation (in the form of either cavity enlargement or rectangular excavations on the bole of the tree) on Red-cockaded Woodpecker trees (n = 202) to that on control trees (n = 110) selected within the cavity tree clusters. Control trees used in this study did not have any cavities and were chosen at random from among those trees in the cluster that were similar in size and age to cavity trees. This aspect of the study was conducted only in the loblolly-shortleaf pine habitat on the northern portion of the Angelina National Forest, and we used chi-square analysis for the comparison.

We noted the aspect of recent Pileated Woodpecker excavation on all cavity trees (n = 785) relative to the orientation of the Red-cockaded Woodpecker cavity. We divided the tree into two longitudinal halves and compared the amount of Pileated Woodpecker excavation on the side containing the cavity to the opposite side of the tree.

We used a chi-square analysis to compare the incidence of recent Pileated Woodpecker excavation on cavity trees in active clusters (n = 123) to cavity trees in inactive clusters (n = 79) in loblolly and shortleaf pine cavity trees, as well as in longleaf pine cavity trees (303 trees in active clusters and 280 trees in inactive clusters). The pine types were compared separately to determine if cover type was related to Pileated Woodpecker excavation rates on Red-cockaded Woodpecker cavity trees.

We also used chi-square analyses to compare the incidence of recent Pileated Woodpecker excavation on active (n = 29) and inactive (n = 94) trees within active clusters in loblolly-shortleaf pine habitat. The same comparisons were made for active (n = 117) and inactive (n = 186) trees within active clusters in longleaf pine habitat. These comparisons were limited to active clusters to reduce any potential cluster site bias from inactive clusters.

We compared the incidence of recent Pileated Woodpecker excavation on trees with naturally excavated cavities (n = 324) to trees with artificial insert cavities (n = 461) using chi-square analysis. For this comparison, we included all cavity trees from active and inactive clusters in both forest types.

We estimated midstory height within the cluster sites to the nearest meter and ranked midstory density from 1 (little or no midstory present within the cluster area) to 5 (extremely dense midstory within the stand). We compared midstory density using a Mann-Whitney U-test and height using a t-test between active and inactive cluster sites in loblolly-shortleaf and longleaf pine habitat types. All statistical tests were conducted at the $\alpha < 0.05$ level and in all cases where we failed to reject the null hypothesis we used a power analyses (effect size = 0.30) to determine if we had an adequate sample (Cohen 1988).

RESULTS

Fifteen (7.4%) of 202 cavity trees in loblolly-shortleaf pine habitat were damaged by Pileated Woodpeckers during the 2- to 3-month period prior to sampling while none of the 110 control trees had been damaged by Pileated Woodpeckers during that time (χ^2 = 8.58, df = 1, P = 0.003). Recent excavations by Pileated Woodpeckers occurred on only the Red-cockaded Woodpecker cavity side on 35 of 41 trees and on both sides of 6 trees, but on no trees was the excavation exclusively on the opposite side of the cavity.

We found no significant difference (test power = 0.99) between the rate of Pileated Woodpecker excavation in active clusters (6 of 123 cavity trees damaged) and that of inactive clusters (9 of 79 cavity trees damaged) in loblolly-shortleaf pine habitat (χ^2 = 2.97, df = 1, P = 0.085). However, we did observe a higher rate of recent excavation in active clusters (19 of 303 cavity trees damaged) compared to the inactive clusters (7 of 278 cavity trees damaged) in longleaf pine habitat (χ^2 = 4.78, df = 1, P = 0.029).

We found no significant difference (test power = 0.91) in the incidence of recent Pileated Woodpecker excavation between active (1 of 29 cavity trees damaged) and inactive trees (5 of 93 cavity trees damaged) within active clusters in loblolly-shortleaf pine habitat (χ^2 = 0.17, df = 1, P = 0.67). We also were unable to detect a difference (test power = 1.00) in the incidence of Pileated Woodpecker excavation in the active (5 of 117 cavity trees damaged) and inactive cavity trees (14 of 186 cavity trees damaged) in longleaf pine habitat (χ^2 = 1.29, df = 1, P = 0.26). We detected no significant difference (test power = 1.00) in the incidence of recent Pileated Woodpecker excavation between trees with a naturally excavated cavity (19 of 324 trees) and an artificial cavity insert (22 of 462 trees, χ^2 = 0.46, df = 1, P = 0.50).

Finally, in loblolly-shortleaf pine habitat we found no significant difference in midstory height between active (mean = 6.1, SE = 0.22) and inactive cluster sites (mean = 8.6, SE = 0.63; t = 0.19, P = 0.19, test power = 0.34), and we found no significant difference in midstory density between active (mean = 2.4, SE = 0.70) and inactive cluster sites (mean = 2.2, SE = 0.32; Mann-Whitney U = 39.5, P = 0.65, test power = 0.45). In longleaf pine habitat, midstory height also did not differ significantly between active (mean = 6.6, SE = 0.94) and inactive cluster sites (mean = 8.7, SE = 1.00; t = −1.44, P = 0.16, test power = 0.52). However, in longleaf pine habitat, midstory was significantly denser in the inactive cluster sites (mean = 3.3, SE = 0.25) than in the active sites (mean = 2.0, SE = 0.17; Mann-Whitney U = 136.0, P = 0.001) due to less intensive management.

DISCUSSION

The apparent attraction of Pileated Woodpeckers to Red-cockaded Woodpecker cavity trees remains unexplained. Observations of Pileated Woodpeckers nesting simultaneously in the same tree with other woodpecker species suggest that their excavation behavior is not directed at the reduction of competition with other species (Hoyt 1948, Schemnitz 1964). Red-cockaded Woodpeckers seem defenseless against Pileated Woodpecker destruction of their cavities. The resin barrier, that is effective in deterring rat snakes from Red-cockaded Woodpecker cavities (Jackson 1974, Rudolph et al. 1990), apparently does not deter Pileated Woodpeckers. Pileated Woodpeckers can fly directly to any portion of the cavity tree without having to cross any resin barrier, and then proceed to damage the cavity entrance and tree.

The presence of dense, hardwood midstory vegetation in the cavity tree cluster may reduce the incidence of Pileated Woodpecker damage on cavity trees by making them harder to find. However, Red-cockaded Woodpeckers tend to avoid areas with a dense hardwood midstory and abandon sites when dense midstory vegetation encroaches (Beckett 1971, Grimes 1977, Conner and Rudolph 1989, Loeb et al. 1992). Thus, Red-cockaded Woodpeckers appear to select the type of habitat that makes them most susceptible to losing cavities to enlargement by Pileated Woodpeckers.

While only 7.4% of the cavity trees we surveyed had signs of recent Pileated Woodpecker damage, this rate could result in a large proportion of cavity trees damaged over time. Saenz et al. (1998) found that more than half of the Red-cockaded Woodpecker cavities in

longleaf habitat that did not have restrictor plates (a metal plate that inhibits cavity enlargement) were rendered unusable by Pileated Woodpeckers. It seems improbable that Red-cockaded Woodpeckers could have evolved in an environment with that rate of cavity enlargement (Conner and Rudolph 1995). We suggest that either the nature or the frequency of the interaction between these two species has changed relatively recently.

We suggest that habitat alteration may have increased the co-occurrence of these two species to a level that is unsustainable for the Red-cockaded Woodpecker. In particular, pine savannahs have been altered greatly by fire exclusion and suppression, which permitted hardwood midstory encroachment in pine-dominated landscapes (Conner and Rudolph 1991, Conner et al. 2001). These anthropogenic changes may have made previously pine-dominated forests more suitable for Pileated Woodpeckers.

Fire-maintained southern pine ecosystems likely had lower densities of snags than that currently available (Conner and Rudolph 1995, Conner et al. 2001). Fires suppression likely has increased the number of snags that Pileated Woodpecker use for nesting and foraging (Conner et al. 1975, Bull and Jackson 1995). Further, the type of fires prescribed during the past several decades (i.e., when humidity is high during cooler months; Brender and Cooper 1968) often are insufficiently intense to ignite snags. These cold, wet conditions different from the hot, dry conditions that likely occurred during naturally occurring wildfires during pre-Columbian times.

The conversion of native longleaf pine savannahs to loblolly and slash (*P. elliottii*) pine plantations during the past 60 years (McWilliams and Lord 1988) has affected snag density in three ways. First, in contrast to naturally low density longleaf pine, loblolly and slash pine plantations are densely stocked, such that there are more trees (potential snags) per given area. Second, the life expectancy of loblolly pine trees is less than half that of longleaf pines; thus the higher death rate of loblolly pines produces more snags per unit time. Finally, loblolly pines are much more vulnerable to southern pine beetle (*Dendroctonus frontalis*) infestation (Hodges et al. 1979; Conner et al. 1997b, 2001), which kills the pines, producing snags that are ideal for Pileated Woodpecker cavity excavation and foraging.

Widespread logging of longleaf pines occurred across the South and into Texas during the late 1800s and early 1900s (U.S. Fish and Wildlife Service 1985, Maxwell and Baker 1983, McWilliams and Lord 1988). Cutover lands either regenerated with loblolly and shortleaf pines by natural seeding or were replanted, usually with loblolly pine. The trees of these relatively unburned, short-lived, second growth loblolly forests now are of sufficient diameter for cavity excavation by Pileated Woodpeckers. Thus, the very high rate of damage to Red-cockaded Woodpecker cavity trees by Pileated Woodpeckers may have occurred during only the last several decades, reflecting the proximity of large loblolly pine snags to Red-cockaded Woodpecker cavity tree clusters.

The use of growing season prescribed burning and restoration of open longleaf pine savannahs likely would reduce the density of snags within Red-cockaded Woodpecker habitat, and thus the density of Pileated Woodpeckers. However, land ownership patterns are problematic in the modern forest landscape. Currently, Red-cockaded Woodpeckers are most prevalent on public land (James 1995) where they have some protection from short rotation timber harvesting. However, these lands typically are not large contiguous blocks, but instead are a mosaic of private and public ownership. Pileated Woodpeckers have large home ranges (Kilham 1976, Mellen 1987) and regularly travel from unmanaged private lands to managed Red-cockaded Woodpecker cluster sites where they destroy cavities. In the current landscape, Red-cockaded Woodpeckers appear to be extremely vulnerable to cavity destruction (Conner and Rudolph 1995, Saenz et al. 1998) and this situation will not improve unless nearby landowners become committed to restoration of open park-like southern pine ecosystems. Otherwise, tools such as artificial cavities to replace lost cavities and restrictor plates to protect existing cavities likely will be required in perpetuity in many populations if the Red-cockaded Woodpecker is to persist.

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HOME RANGE, MOVEMENT, AND NESTING OF LEAST BITTERNS IN WESTERN NEW YORK

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ABSTRACT.—We studied the nesting ecology of Least Bitterns (*Ixobrychus exilis*) during 1999 and 2000 within an 8,000-ha wetland complex in western New York. We used radio telemetry to track 33 adult Least Bitterns to locate nests and determine movement patterns, and 12 chicks to determine postfledging movements. Least Bittern Mayfield nest success rates were 43.8% (n = 38) in 1999 and 52.5% (n = 35) in 2000, and they renested and had double broods. Mean home range of adults was 9.7 ha (n = 33), but varied (range = 1.8–35.7 ha) depending upon whether birds used one or two areas during the breeding season. The mean movement of chicks from their nests was 13.4 m between capture and 23 days posthatching (n = 11), and 29.4 m when 24–27 days old (n = 4). Mean age at first flight was about 29 days old (n = 4). Vegetational structure and composition and marsh size appear to be important factors to consider when managing for Least Bittern populations. *Received 15 August 2001, accepted 23 April 2002.*

Research on the breeding biology of the Least Bittern (*Ixobrychus exilis*) has focused on nesting habitat, reproductive success, nesting behavior, and demographic characteristics (Kent 1951, Weller 1961, Frederick et al. 1990, Ziebell 1990, Post and Seals 1993, Post 1998, Rodgers and Schwikert 1999, Lor 2000). However, there still are significant gaps in our knowledge of this secretive marsh bird. For example, there is no information on Least Bittern home range and movement during the breeding season (Gibbs et al. 1992a), yet such information is necessary to determine habitat size and distributional requirements. Gibbs et al. (1992a) also noted the lack of information on the ability to renest and on juvenile dispersal patterns. Several researchers (Kent 1951, Weller 1961, Ziebell 1990; C. R. Paine unpubl. data) have suggested that Least Bitterns renest (initiate a new nest and clutch after a previous nest is unsuccessful) and have double broods (produce a second nest and clutch after a first clutch has hatched), but there has been no conclusive evidence from marked birds.

Finally, Least Bittern chicks (a bird between hatching and first flight) first leave their nest when between 5 and 9 days old, but they continue to return to the nest area for several days (Nero 1950, Weller 1961). Hence, because Least Bittern chicks are very mobile at a young age and are difficult to monitor because they use dense vegetation (Rodgers and Schwikert 1999), little is known about their postfledging movements. In this study, we define fledging as when the chicks are no longer predictably associated with their nest area (>5 m away), which usually occurred between 12 and 18 days old.

These gaps in knowledge are especially significant because the Least Bittern is listed by the U.S. Fish and Wildlife Service as a Species of Management Concern (U.S. Fish and Wildlife Service 1995) and has a state listing ranging from indeterminate to threatened in 9 of 13 northeastern states (Gibbs and Melvin 1992). The Least Bittern currently is listed as threatened in New York State. Hence, more information on many aspects of Least Bittern breeding biology clearly is needed to facilitate the design of appropriate management and conservation plans.

We used radio telemetry to track individual birds to examine aspects of Least Bittern breeding biology that have not been studied in detail. Our main objectives were (1) to calculate nesting success and determine if Least Bitterns renest or have double broods, (2) to determine home range and general movement patterns during the breeding season, and (3) to determine postfledging chick movements and age at first flight. We also provide information on other aspects of Least Bittern

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breeding biology and natural history, including clutch size and nesting habitat.

STUDY AREA

We studied Least Bitterns between late April and late August, 1999–2000, within an 8,000-ha wetland complex in western New York composed of the Iroquois National Wildlife Refuge and the Oak Orchard and Tonawanda state wildlife management areas. The complex is located in the northern part of the Least Bittern breeding range (Gibbs et al. 1992a) in the Great Lakes Plain ecozone of New York State (Andrle and Carroll 1988), about 27 km south of Lake Ontario and 56 km east of Lake Erie (43° 07′ N, 78° 22′ E). This wetland complex consists of 60% wetlands (including 17% emergent marsh, 26% flooded timber, 12% open water, and 5% scrub-shrub marsh) and 40% grasslands, forests, early successional forests, or fallow fields (Lor 2000).

We conducted trapping and subsequent tracking and nest searching at eight emergent marshes: Oxbow (57 ha; 45% emergent vegetation, 55% open water), Goose (45 ha; 70% emergent vegetation, 30% open water), Paddy 1 (20 ha; 50% emergent vegetation, 50% open water/flooded timber), Paddy 2 (23 ha; 75% emergent vegetation, 25% open water), Ruddy (140 ha; 65% emergent vegetation, 35% open water), Olson South (12 ha; 45% vegetation, 55% open water), Cayuga (148 ha; 40% vegetation, 60% open water), and Knowlsville (19 ha; 35% vegetation, 65% open water). Ratios of emergent vegetation to open water are visual approximations we made during August 2000 from marsh edges and from a canoe. The dominant emergent vegetation in all marshes was cattail (*Typha* spp.). Other types of emergent vegetation included bur-reed (*Sparganium* spp.), hard-stemmed bulrush (*Scirpus acutus*), swamp loosestrife (*Decodon verticillatus*), and purple loosestrife (*Lythrum salicaria*).

METHODS

Trapping and radio attachment.—We trapped 57 of 70 (81%) adult Least Bitterns by broadcasting the male "cooing" vocalization (Bent 1926) from a tape recorder placed at water level in the center of a row of mist nets. We obtained vocal recordings from either the Peterson field guide series *More birding by ear: eastern/central* (Walton and Lawson 1994) or *Stokes field guide to bird songs: eastern region* (Elliot et al. 1997) and created 1-min continuous loop tapes with alternating periods of about 15 s of calling and 15 s of silence. Within a marsh, we usually operated 1–2 set-ups, each consisting of 1–6 nets and a tape player. We sometimes targeted individual birds by setting nets where a male was observed calling.

We also trapped 11 adult Least Bitterns (17%) by setting up 2–8 nets in a "U" shape around one end of a stand of vegetation and having 3–8 people walk through the vegetation to flush birds into the nets. We also hand captured two females on their nests. For all birds captured, we measured wing chord, beak length, and tarsus, and we weighed, determined sex via plumage color (Gibbs et al. 1992a), banded, radio marked, and released them at the trap sites.

During 1999, we fitted 2.28-g radio transmitters (Advanced Telemetry Systems, Isanti, MN) onto the backs of Least Bitterns between the wings by using either epoxy attached to the feathers (18 birds) or cyanoacrylate glue (super glue) attached to the skin (7 birds). We also attached radio transmitters to 12 birds by sewing and gluing the radio transmitters to a Herculite-laminated fabric (Herculite Protective Fabrics Corp., New York) bib fitted around the bird's neck under the chest feathers (Brininger 1996).

During 2000, with the exception of one radio transmitter attached with super glue, we attached 2.36-g radio transmitter packages between the wings on each bird's back with a stainless steel anchor-shaped wire inserted subcutaneously as described by Pietz et al. (1995). We modified the procedure by using super glue instead of sutures to hold the radio transmitter in place. Hence, the anchor simply was threaded through an incision made via a hypodermic needle, super glue was applied to the base of the radio transmitter, the radio transmitter was pressed onto the skin for several seconds until the glue dried, and a drop of super glue was used to seal the incision. It was not necessary to trim any feathers around the attachment site. Radio packages in both years never exceeded 3.5% of body mass.

Overall handling time of birds once removed from nets usually was ≤15 min. All trapping and handling followed the Ornithological Council guidelines (Gaunt and Oring 1997) and an Animal Welfare Protocol Statement at the State Univ. of New York, College of Environmental Science and Forestry.

We captured chicks between 12 and 18 days old by searching the vegetation surrounding nest sites. During 1999, we only banded chicks, but during 2000 we equipped one chick that weighed >65 g from each of 12 nests with a 1.3-g radio transmitter; radio transmitters never exceeded 2% of a chick's current body mass. We attached radio transmitters between the wings by applying a drop of super glue to the surface of the radio transmitter and holding it against the skin. Care was taken not to glue the radio transmitter to feathers. Chicks usually were handled for ≤10 min and released near their nest.

Nesting.—To locate nests, renests, and second nests, we homed on radio-marked Least Bitterns found in the same general location ≥5 days in a row. We also conducted nest searches in areas where radio-marked Least Bitterns were suspected of nesting. Nest searches were conducted by 1–5 people systematically wading back and forth through the marsh within about 3–10 m of each other. We marked nests with flagging tied to the tallest piece of vegetation within a few meters of the nest. We determined approximate hatching dates by floating eggs (Hays and LeCroy 1971), and we checked nests every 1–9 days to determine their fate. We determined nest initiation dates by backdating from hatching, assuming an incubation period of 19 days (Weller 1961). We recorded the vegetation used

for nest construction for most nests. For most nests located during 1999, we also recorded water depth under the nest and distance to the closest water pool ≥3 m in diameter.

We used the Mayfield method (Mayfield 1961, 1975) to calculate daily survival, nest success (for the period when eggs but not chicks were in the nest), and fledging success (for the period after the first egg hatched until the first chick was 12 days old). We chose 12 days because chicks began to leave the nest area at 12 days posthatching, and it became difficult to determine if an absence of chicks near the nest site meant chicks had left the nest area or were dead. We calculated standard errors and 95% confidence intervals, and performed tests to compare daily mortality rates using methods developed by Johnson (1979).

Home range and movement of adults.—We located radio-marked adult Least Bitterns 5–7 times per week by using triangulation with 3-element hand-held Yagi antennas. Consecutive locations on a single bird always were ≥12 h apart, following the protocol of White and Garrott (1990). To assure accuracy, observers in contact via 2-way radio simultaneously took compass bearings when both received clear signals and the bearings were at approximately right angles from each other and as close to the bird as possible. Over the course of 2-week periods, we monitored locations evenly during 2-h time blocks from 05:00–07:00 and from 22:00–05:00 EST.

We tested for observer error by placing additional radio transmitters in marshes used by radio-marked Least Bitterns. Observers took compass bearings of these radio transmitters from existing stations, using the same techniques used in routine tracking, except there were no discussions of radio transmitter locations via 2-way radio, and no movement to other stations if signals were unclear due to radio wave reflection or diffraction (Samuel and Fuller 1994). All technicians who participated in the radio telemetry portion of the study were tested.

The mean absolute angular error of 128 bearings was 8.3° ± 0.6 SD after eliminating extreme outliers (angular errors >25°, $n = 11$) (Lee et al. 1985). We eliminated these outliers because such errors were highly unlikely during actual data collection due to the use of the 2-way radios and ability of observers to move when signals were unclear or there was strong reflection or diffraction of radio waves (Samuel and Fuller 1994). The mean antennae-to-animal distance (AAD; Gould and Jenkins 1993) of a random sample of 35 bird locations was 191.9 m. When we used the mean angular error and the mean AAD, the mean estimated distance error from plotted to actual transmitter location was 27.9 m. When we used the methods from Lee et al. (1985) and White and Garrott (1990), bias was −0.5°, and the mean 95% confidence bearing arc (±1.96 SD) was ±20.4°. The mean 90% error polygon determined from two error arcs intersecting at right angles at mean AAD from two stations was 2.1 ha.

We calculated bird location coordinates using the program LOCATE II (Nams 1990), and we estimated home range for individuals via the fixed kernel method (Worton 1989) of the animal movement extension to ARCVIEW (Hooge et al. 1999). We used least squares cross validation to automatically select the bandwidth (smoothing parameter). We used the cross-validated fixed kernel home range estimator because it is the most accurate; Seaman and Powell (1996) found that the cross-validated fixed kernel home range was better than the harmonic mean estimator, which Boulanger and White (1990) found to be the least biased of the common home range estimators, including Fourier series, harmonic mean, minimum convex polygon, and two different 95% ellipse home range estimators. We calculated both the 95% utilization distribution, which we refer to as "home range," and the 50% utilization distribution, which we refer to as "core range." Calculations were done only on individuals with ≥30 locations (Seaman et al. 1999).

We also examined movement patterns by constructing plots of locations by date. The maximum distance between any two locations also was calculated for each bird using the animal movement extension to ARCVIEW (Hooge et al. 1999).

To examine differences in marsh size between sexes for home range, core range, and maximum distance between locations, we divided birds into four groups according to their sex and whether they were in marshes or groups of marshes >100 ha, or in relatively isolated marshes <60 ha. We chose these size categories based on the size distribution of marshes in the complex. Individual marshes were considered grouped if only a narrow dike separated adjacent marshes. In contrast, relatively isolated marshes <60 ha were still in the overall marsh complex but were separated from other marshes by more than a narrow dike (≥50 m distance and with barriers such as roads, tree rows, forested areas, or fields). There were three relatively isolated marshes <60 ha (57, 45, 19 ha) and two marshes or groups of marshes >100 ha (Group 1 included three individual marshes of 148, 12, and 4 ha that were used by radio-marked Least Bitterns; Group 2 included four individual marshes of 140, 20, 23, and 12 ha also used by radio-marked Least Bitterns, and two marshes of 142 and 20 ha that were not used by radio-marked Least Bitterns).

Using the Shapiro-Wilk test (Conover 1980), we determined that home range, core range, and maximum distance between locations data were not normally distributed even after a $\log_{10}$ transformation. We therefore used Mann-Whitney 2-sample tests (Conover 1980) to test for differences between males and females (with marsh sizes combined), and among marsh sizes (with sexes combined) for home range, core range, and maximum distance among locations. We also used Mann-Whitney tests to examine differences in home range, core range, and maximum distance between two locations for females in the two marsh size categories, males in the two marsh categories, males and females

TABLE 1. Reproduction estimates of Least Bitterns at Iroquois National Wildlife Refuge and Tonawanda and Oak Orchard state wildlife management areas wetland complex, western New York, in 1999 and 2000.

	Year	Number of successful nests	Number of failed nests	Exposure days	Daily survival		Nest success	95% confidence interval (%)
					Mean	SE		
Nest success	1999	27	9	320.5	0.972	0.009	58.2%	40.4–83.2
	2000	24	6	296.5	0.980	0.008	67.8%	49.3–92.9
Fledging success	1999	23	4	174	0.977	0.011	75.6%	57.0–99.7
	2000	23	5	237.5	0.979	0.009	77.5%	61.5–97.1
Overall success	1999	25	13	494.5	0.974	0.007	43.8%	27.6–69.0
	2000	24	11	534	0.979	0.006	52.45%	35.5–77.2

in marshes <60 ha, and males and females in marshes or groups of marshes >100 ha.

Movement of chicks.—We located radio-marked chicks by homing on their radio signal every 3–7 days after capture to determine the distance from their nest. To minimize chick disturbance, we usually approached no closer than 5–10 m. If a chick was in the same location on two consecutive checks, however, we approached it until we could determine if the transmitter had detached or the bird had died. If a chick reached flight stage and left the nest area, we monitored its location using triangulation from the marsh edge. We monitored chicks until either their radio transmitters fell off, the signals were lost, or until 31 August.

RESULTS

Trapping.—During 1999, we radio marked 36 adult Least Bitterns (16 males and 20 females). The largest number of adults (12) was trapped in Oxbow Marsh, followed by 3–6 adults trapped at six other marshes. The majority of the radio transmitters fell off (including all radio transmitters attached with epoxy); thus, only nine birds were radio tracked long enough to obtain ≥30 locations. We recaptured two of the 36 adults later in the same season, both females.

During 2000, we radio marked 32 adults (17 males, 15 females). Eight adults were captured in both Oxbow Marsh and Ruddy Marsh, followed by 2–6 trapped in five other marshes. We tracked 24 adults long enough to obtain ≥30 locations. We recaptured one male trapped earlier in 2000, but we did not recapture any birds banded in 1999. We also radio marked 12 chicks.

Nesting.—We found 51 nests during 1999 and 41 nests during 2000 that contained chicks, eggs, or egg fragments. During both years, the largest number of nests was found in Oxbow Marsh (1999: 15 nests; 2000: 17 nests), followed by Ruddy Marsh (1999: 11 nests; 2000: 9 nests). Other marshes contained 1–9 nests. During 1999, we found nests of four radio-marked birds (two male and two female, including one pair). During 2000, we located 14 nests of radio-marked males and 9 nests of radio-marked females. We observed a radio-marked male copulating with a female on their nest, which contained an incomplete clutch of two eggs.

Mean clutch size was 5.25 eggs ± 0.11 SE (range: 3–6, $n = 64$). There were 30 nests with 6 eggs, 23 with 5, 8 with 4, and 3 with 3. The time from laying the first egg to hatching the first egg ranged from 19–21 days ($n = 5$ nests).

Of the total nests located during 1999 and 2000, the majority (77%, $n = 84$) were constructed exclusively of cattail, but nests also were made from bur-reed (13%), bur-reed and cattail (4%), grasses and cattail (2%), hard-stemmed bulrush (1%), swamp loosestrife (1%), and purple loosestrife (1%). Water level at nest sites during 1999 ranged from 0–57 cm with a mean of 34.4 cm ± 2.1 SE ($n = 33$). The mean distance to open water from nest sites was 3.5 m ± 0.8 SE ($n = 36$). Nest initiation began in early May and continued until early July during 1999, and began in mid-May and continued until mid-July 2000.

Fledging success was higher than nesting success during both 1999 and 2000 (Table 1), but the longer period for nest success (19 days) than for fledging success (12 days) can account for this result. Daily survival rates for the two periods were not significantly different (1999: $Z = 0.348$, $P = 0.73$, 2000: $Z = 0.659$, $P = 0.95$). The combined overall suc-

TABLE 2. Movements of radio-marked Least Bitterns at Iroquois National Wildlife Refuge and Tonawanda and Oak Orchard state wildlife management areas wetland complex, western New York, were small but highly variable in 1999 and 2000.

	Core range (ha)		Home range (ha)		Maximum distance between two locations (m)	
Group	Mean	SE	Mean	SE	Mean	SE
All adults	1.4	0.3	9.7	1.5	393	35.7
Males	1.0	0.3	8.1	2.2	307	34.8
Females	1.8	0.5	11.4	2.1	485	56.0
Marshes <60 ha	1.1	0.3	7.5	1.5	360	53.5
Marshes >100 ha	1.6	0.4	11.6	2.4	421	48.3

cess rates for the 31-day period were 43.8% during 1999 and 52.5% during 2000. We attributed most nest failures to predation, although we also suspected some nests were deserted, and at least one nest was destroyed by strong winds.

During 2000, we observed both renesting and double brooding. In one instance we observed a radio-marked individual (male 713) on one nest, and after that nest was depredated, on a second nest. In two instances of double brooding we observed two radio-marked individuals (male 913 and female 942, not a pair) on first nests, and after those nests hatched, on second nests. We suspect two additional instances of renesting (male 892 and female 752, not a pair) and two additional instances of double brooding (female 831 and male 733, not a pair) because we observed radio-marked individuals on first nests and we subsequently flushed them from the immediate vicinity of different nests. The mean time between failure or hatching of the first nest and initiation of a new nest was 5.3 days ± 0.9 SE (n = 3) for renesting birds, and 21.7 days ± 3.5 SE (n = 3) for double-brooding birds. The mean distance separating the two nests was 106.8 m ± 38.2 SE (n = 3) for renests and 213.6 m ± 94.1 SE (n = 4) for double broods.

Home range and movement of adults.—We obtained 1,407 locations for 33 adult Least Bitterns (17 males and 16 females). Least Bitterns usually did not leave the marsh where they were trapped unless there were adjacent marshes separated only by a narrow dike. In the Tonawanda State Wildlife Area, where several marshes were separated only by dikes, we detected 12 of 15 birds (80%) moving among marshes at least once. In contrast, there were only two separate incidents in which birds from relatively isolated marshes <60 ha were detected moving from the marsh where they had been trapped.

Mean home range size was 9.7 ha ± 1.5 SE (range = 1.8–35.7 ha, n = 33), and mean core range was 1.4 ha ± 0.3 SE (range = 0.2–8.0 ha, n = 33; Table 2). Overlapping home ranges were common. In Oxbow Marsh, for example, home ranges of four radio-marked males and three radio-marked females overlapped. The mean home range of adult females was 3.3 ha larger than that of adult males (Mann-Whitney U = 81.00, P = 0.049). Least Bitterns in marshes or groups of marshes >100 ha had a larger mean home range than Least Bitterns in marshes <60 ha, but the difference was not significant (U = 104, P = 0.27; Table 2). None of the other home range and core range parameters were significant: core range of males and females (U = 88.00, P = 0.87), core range and marsh sizes (U = 110, P = 0.38), females by marsh size categories (home range: U = 24.00, P = 0.44; core range: U = 30.00, P = 0.88), males by marsh size categories (home range: U = 26.00, P = 0.42; core range: U = 19.00, P = 0.13), males versus females for relatively isolated marshes <60 ha (home range: U = 14.00, P = 0.12; core range: U = 14.00, P = 0.12), and males versus females for marshes or groups of marshes >100 (home range: U = 25.00, P = 0.20, core range: U = 31.00, P = 0.46).

The mean maximum distance between two locations for all adults was 393 m ± 36 SE (range = 172–801 m, n = 33; Table 2), but this distance was 179 m longer for females

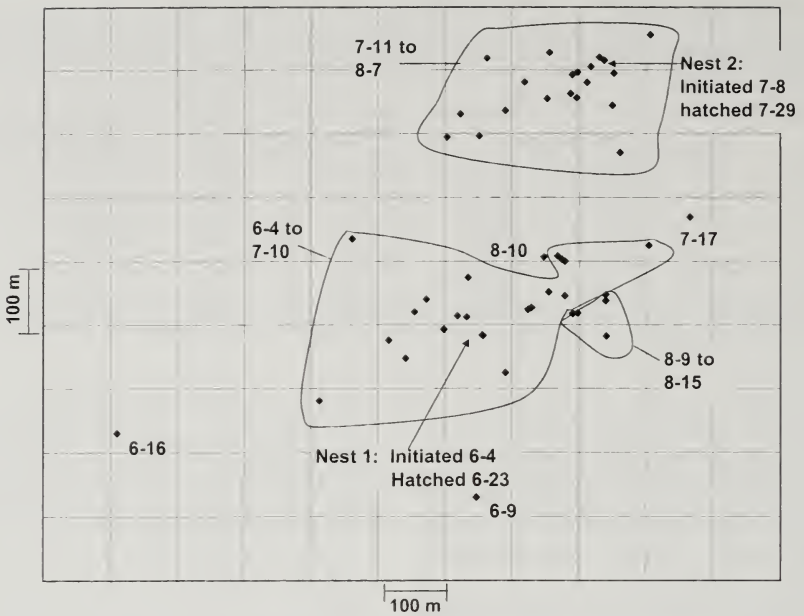

FIG. 1. Least Bittern male 733 was double brooded and used two distinct areas in Ruddy Marsh, Tonawanda State Wildlife Management Area, western New York. Locations were from 4 June to 15 August 2000; home range = 29.7 ha and maximum distance between two locations = 718 m.

than for males (U = 77.00, P = 0.034). In addition, maximum distance between two locations was 123 m longer for males in marshes or groups of marshes >100 ha than for males in relatively isolated marshes <60 m (U = 13.00, P = 0.033).

The shape of home ranges and the movement among Least Bitterns varied markedly. Six birds (15%) each used two distinct areas during the breeding season. For example, male 733 was double brooded with a nest in each of two areas of Ruddy Marsh (Fig. 1). The remaining birds were located primarily in one area, but the size of these areas varied greatly. For example, all the locations for male 782 were close to his one nest (home range = 2.6 ha); male 913 had two successful nests 29.3 m from each other in a single cattail clump (home range = 5.5 ha); and male 792, with one verified nest, used one large area (home range = 13.7 ha). Females 942 and 752 (each had two nests) used one general area but shifted use over time from one part of their range to another (Fig. 2). About 50% of females initially moved either within one marsh or among marshes before settling into one area for the remainder of the season (Fig. 3), and 39% of birds made at least one trip away from their usual home range areas.

Movement of chicks.—Of 12 chicks fitted with radio transmitters, six lost their radios before attaining flight. Another chick was depredated at 19 days of age (we found the carcass). One fledgling was not included in the calculations because its age at capture was not known. Of the remaining four birds, mean distance from nests was 13.4 m ± 1.8 SE (n = 11) between capture and 23 days posthatching. Between 24 and 27 days of age, chicks wandered ≤60 m but the mean distance from their nests was only 29.4 m ± 10.5 SE. At this stage, chicks could move quickly through vegetation, but they probably were not yet able to fly. Age at first flight for individual birds could not be determined exactly because birds were not monitored on a daily basis, but the approximate mean age of the four birds retaining radio transmitters at first flight was 29 days. They initially made short flights within the marsh where they hatched, and then three of five left the

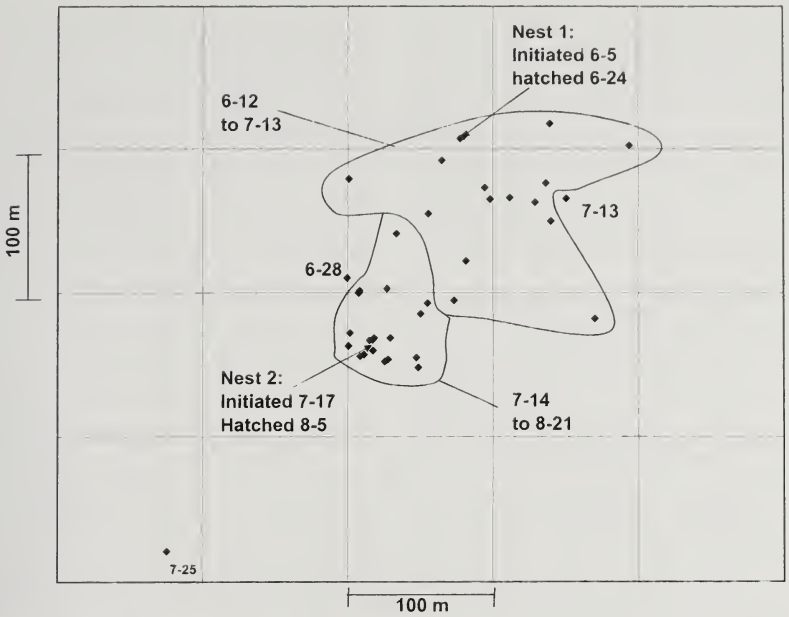

FIG. 2. Least Bittern female 942 was double brooded, used one general area, but shifted use within that area in Oxbow Marsh, Oak Orchard State Wildlife Management Area, western New York. Locations were from 12 June to 21 August 2000; home range = 2.8 ha and maximum distance between two locations = 203.7 m.

marsh ≤8 days of first flight. The two remaining birds lost their radios shortly after first flight. We were able to relocate only one bird after leaving its natal marsh. This bird was flying within its natal marsh when 27–28 days old, but at 30–31 days had traveled 1,800 m to another marsh. When 37–39 days old, we observed this bird standing on a stick in shallow (<10 cm) water in an area of sparse cattail mixed with purple loosestrife and flooded timber.

DISCUSSION

During the 2000 field season, we did not recapture any of the 48 Least Bitterns trapped during 1999, which suggests either low return rates or low survival. There have been documented returns of other marsh birds, such as the American Bittern (*Botaurus lentiginosus*) (Brininger 1996, Azure 1998) and the Virginia Rail (*Rallus limicola*) (Mousley 1931), to the same breeding areas, but there is no information on philopatry in Least Bitterns (Gibbs et al. 1992a). More intensive trapping of birds for several years likely is required to examine philopatry in Least Bitterns.

Nesting.—The relatively large mean clutch size of 5.25 eggs and the large percentage of 6-egg clutches (46.9%) we documented suggests latitudinal variation. Mean clutch size was 4.08 eggs ± 0.59 SD in Florida (n = 104; Rodgers and Schwikert 1999), 3.80 eggs ± 0.78 SD in South Carolina (n = 110; Post 1998), 4.39 eggs ± 0.43 SD in Iowa (n = 59; Weller 1961), and 4.6 eggs ± 0.76 SD in Wisconsin (n = 35; Ziebell 1990). No clutches larger than five eggs were observed in either South Carolina (Post 1998) or Florida (Rodgers and Schwikert 1999). Increasing clutch size with latitude may be explained by Ashmole's hypothesis (Ashmole 1963, Ricklefs 1980), which suggests that clutch size is determined by the ratio of available resources during the breeding season to the demand for these resources by breeding adults.

Consistent with other studies (Weller 1961, Ziebel 1990, Post and Seals 1993, Lor 2000), we found that the majority (83%) of Least Bittern nests were at least partially constructed from cattails. Bur-reed (17% of nests) and hard-stemmed bulrush (1%) were

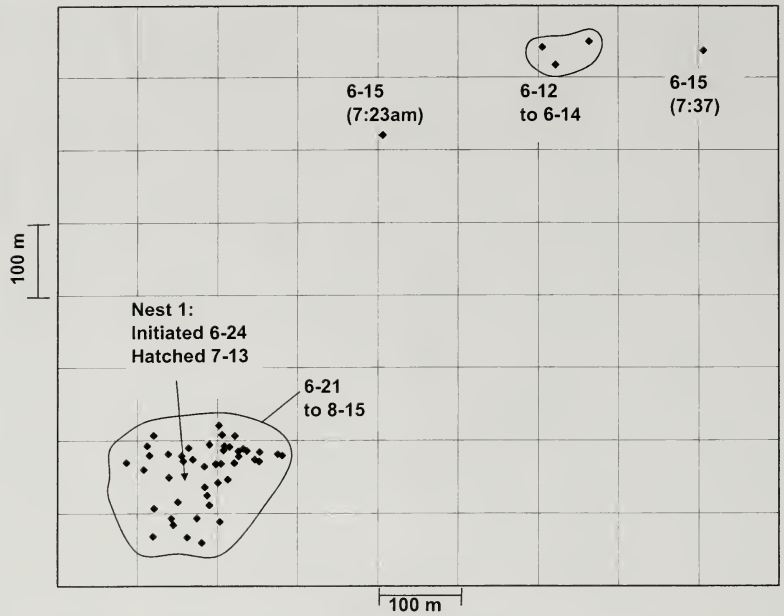

FIG. 3. Least Bittern female 173 moved around for a week before settling into one area where she had one nest in Goose Marsh, Oak Orchard State Wildlife Management Area, western New York. Locations were from 12 June to 15 August 1999; home range = 7.9 ha and maximum distance between two locations = 792 m.

used to a lesser extent than cattail, probably at least partially due to differences in availability, but Rodgers and Schwikert (1999) found soft-stemmed bulrush (*Scirpus validus*) was used for construction of 52% of nests (n = 207) in Florida, and Kent (1951) found most nests in Iowa were located either in bur-reed (58%) or soft-stemmed bulrush (37%; n = 19). In Florida, Kushlan (1973) and Frederick et al. (1990) found that sawgrass (*Mariscus jamaicensis*) was an important nesting substrate. Frederick et al. (1990) suggested that the main reason Least Bitterns usually are found in cattail in northern states is because cattail is among the few tall plants in the North to grow in high densities in deep water.

Our nest success rates were 58.2% in 1999 and 67.8% in 2000. Other studies of Least Bitterns reported Mayfield nest success estimates of 80% (n = 16) and 46% (n = 37) in the same study area as ours (Lor 2000), 37% (n = 49) in Illinois (C. R. Paine unpubl. data), and 54.9% (n = 159) in South Carolina (Post 1998). Least Bitterns often nest over water and away from shore, making them less vulnerable to land predators. However, there still are numerous potential predators of Least Bittern young and eggs, including American Crows (*Corvus brachyrhynchos*), raptors, blackbirds, Blue Jays (*Cyanocitta cristata*), snakes, and turtles (Bent 1926, Weller 1961), and raccoons (*Procyon lotor*; Ziebell 1990). As in other studies (Ziebell 1990, Lor 2000), Marsh Wrens (*Cistothorus palustris*) were suspected egg predators because of the small puncture holes found in some eggs during our study. We also suspected that some nests were depredated by mink (*Mustela vison*).

Our study is the first to confirm instances of renesting and double brooding in Least Bitterns based on marked individuals, although more information is needed to determine the proportion of birds that renest or have second broods. Our study suggests that a minimum of 17% (3 of 24) of Least Bitterns produced double broods and 60% (3 of 5) renested. Second nests were not necessarily near first nests: one renest was 165 m from the first nest, and another was 475 m distant.

Home range and movement.—Although our

radio telemetry error was relatively high when determining the location of individual Least Bitterns, the level of accuracy was adequate to determine the approximate home range and movement patterns. Actual error probably was not as high as that determined from error testing because observers had the ability to move to a new station if signals were not clear, and they could discuss the location of birds via two-way radio. In addition, because the antennae-to-animal distance almost always was small, the effect of degree error was small (estimated mean = 29.7 m).

Adults.—The mean home range size of Least Bitterns was only 9.7 ha. One possible factor contributing to small home range size is that Least Bitterns seem to feed primarily in the area surrounding their nest. For example, Weller (1961) observed Least Bitterns catching prey items from their nests as they incubated, and hunting in the water surrounding their nest. We observed many cases of vegetation bent over to form a feeding platform in dense cattail clumps that also contained Least Bittern nests. By gripping emergent vegetation and using these feeding platforms, Least Bitterns are able to feed over deep water near their nests (Gibbs et al. 1992a). Other small marsh birds have even smaller home ranges. For example, home range estimates for Sora and Virginia Rails were 0.2 ha (Johnson and Dinsmore 1985), and a home range estimate for Pied-billed Grebes (*Podilymbus podiceps*) was 1.3 ha (Glover 1953). The American Bittern uses similar freshwater wetland habitat as the Least Bittern, but has much larger home ranges (mean breeding home range = 210 ha; mean postbreeding home range = 183 ha; Azure 1998). This larger home range probably is a result of the male American Bittern not incubating eggs or caring for young, nests that sometimes are located in upland cover adjacent to wetlands (Gibbs et al. 1992b), its larger body size (mean male weight = 906 g, n = 28; mean female weight = 580 g, n = 17; Brininger 1996), and greater food requirements.

The large variation in Least Bittern home range size (1.8–35.7 ha) may have been influenced by birds using two distinct areas during the breeding season. For example, the three largest home ranges belonged to males 733 (29.7 ha) and 762 (31.6 ha), and female 843 (35.7 ha); all used two distinct areas during the breeding season. Whether birds use two areas or stay in one area could depend upon factors such as food availability, nesting substrate, and whether they produce double broods.

Both home range and maximum distance between locations were larger for females than males, a difference likely due to the stage of the breeding cycle when birds were trapped. Due to the nature of the trapping method (using broadcasts of male vocalizations), males most likely were trapped while defending an established nesting territory, whereas females (except those captured on nests) probably were trapped while in search of a mate. Therefore, perhaps some females were located in a number of different locations before they settled into an area. In some cases, Least Bitterns may spend a large portion of the breeding season in search of a mate. For example, a female trapped in Oxbow Marsh on 29 May, and then again 20 days later in Goose Marsh, was responding to the broadcast of a male call.

Overall, marsh size was not associated with home range size or maximum distance between two locations. Differences may not have been significant, however, because the marshes in the <60 ha marsh category were not very small (19–56 ha). The only significant difference related to marsh size was that males in marshes or groups of marshes >100 ha had a greater maximum distance between locations than males in the isolated marshes <60 ha. This finding may be a result of males in larger marshes having a larger area for foraging and being able to initiate second nests farther from initial nests. Brown and Dinsmore (1986) and Gibbs et al. (1991) found that both marsh size and isolation were important factors determining bird species richness in wetlands. In particular, Brown and Dinsmore (1986) suggested that Least Bitterns possibly were area dependent because 92% of Least Bitterns were observed in marshes ≥5 ha. Lor (2000), in the same study area as ours, found that although Least Bitterns were detected in marshes of all three size categories (1–41 ha, 41–100 ha, 101–155 ha), they were more abundant in marshes 41–100 ha than in marshes 1–41 ha. She at-

tributed this finding, however, primarily to the vegetation composition and structure in Oxbow Marsh, which was in the 41–100 ha category and where Least Bitterns were particularly abundant.

Vegetation type and cover ratios likely are even more important than marsh size for Least Bittern populations. This wetland complex has a large overall population of Least Bitterns, probably in large part due to the many marshes with a high level of interspersion of water and tall, emergent vegetation (primarily cattail). For example, Oxbow Marsh, which had the highest number of nests found and the most birds trapped, was composed of clumps of dense cattail surrounded by open water with an approximate interspersion of 45% emergent vegetation to 55% open water. Weller and Spatcher (1965) found that Least Bitterns nested only in sturdy emergents over water and reached their highest numbers in hemi-marshes (50% water to 50% cover). In fact, they observed that Least Bitterns did not use an area of dense vegetation at all until muskrats (*Ondatra zibethica*) removed considerable vegetation to create a hemi-marsh condition. Weller and Spatcher (1965) also observed maximum bird density and diversity in hemi-marshes, and Gibbs et al. (1991) found that wetlands in Maine with an intermediate level of emergent cover (33–66%) were used by more species than wetlands with cover levels of either >66% or <33%. Nelson and Kadlec (1984) synthesized considerable information on the hemi-marsh concept, noting that attractiveness to birds may relate to production of invertebrates through the growing season.

Chicks.—Similar to Nero (1950), we found that Least Bittern chicks first left the immediate vicinity of their nest when 12–18 days old. When 24–27 days old, they were located a mean distance of 29 m from the nest. Although chicks probably are fed by their parents until able to fly (Palmer 1962), a certain degree of dispersal from the nest area before flight likely is an adaptation to limit predation of all offspring from a nest.

Whereas adult Least Bitterns were not found far from the marsh where they were trapped, three of five birds that retained radio transmitters until capable of flight left their natal marsh within 8 days of first flight. Young Least Bitterns may disperse because they require different types of habitat for foraging than their nest areas can provide. For instance, areas with shallow water may provide easier, more efficient foraging for young birds; the one bird that was relocated after it left its natal marsh was observed standing in water <10 cm deep. Fledgling movements in other bird species may serve to assess possible future breeding sites and to aid in muscle development (Reed and Oring 1992), both of which also could be true of Least Bitterns.

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WINTER HOME RANGE AND HABITAT USE OF FEMALE NORTHERN SAW-WHET OWLS ON ASSATEAGUE ISLAND, MARYLAND

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ABSTRACT.—We quantified home range size and habitat selection of seven female Northern Saw-whet Owls (*Aegolius acadicus*) on Assateague Island, Maryland, during the winters of 1996 and 1997. Home range size (95% fixed kernel) was 103.5 ha (± 50.3 SE). Home range size increased with time spent radio tracking as biweekly home ranges were smaller than those calculated for longer time periods. Home ranges often overlapped in time and space and in one instance the home range for one owl was completely within that of another owl. Northern Saw-whet Owls used primarily pine woods and shrub swamp habitats, with pine woods used more often than any other habitat type and significantly more than expected based on habitat availability. *Received 7 June 2001, accepted 26 February 2002.*

The east coast of the United States is a migration corridor for Northern Saw-whet Owls (*Aegolius acadicus*); they commonly are captured and banded at coastal migration sites, including Cape May in New Jersey (Duffy and Kerlinger 1992), Assateague Island in Maryland (Brinker et al. 1997), and Cape Charles in Virginia (Whalen et al. 1997). Coastal shrub habitat may be important as stopover sites during migration and as wintering habitat (Loos and Kerlinger 1993). Little is known, however, about wintering habitat and ecology of Northern Saw-whet Owls, particularly from coastal islands. The only published studies from coastal islands involved winter food habits (Holt et al. 1991) and winter roost sites (Churchill et al. 2000).

We radio tagged and monitored Northern Saw-whet Owls at Assateague Island, Maryland, to quantify winter home range and habitat use. Habitat on the island differs in structure and species composition from the mainland, and the island vegetation is unusual compared to breeding habitat in boreal forests (Cannings 1993, Churchill 1998). The main objectives of this study were to determine winter home ranges of Northern Saw-whet Owls, estimate overlap among individual home ranges, and to examine habitat use and selection on Assateague Island.

STUDY AREA AND METHODS

We conducted the study on a 1,621-ha portion of Assateague Island (38° 10′ N, 75° 10′ W) in Worcester County, Maryland. The ocean side of this coastal barrier island is an interdunal grassland (10% of the study area) sparsely vegetated with herbaceous plants and shrubs including beach plum (*Prunus maritimus*), beach grass (*Ammophila breviligulata*), and bayberry (*Myrica cerifera*). Another 9% is intertidal beach and bare sand. The bay side is an extensive tidal marsh (*Spartina alterniflora*, *S. patens*, *Distichlis spicata*; 36%), some of which grades into myrtle shrub swamp (*Myrica pensylvanica*; 36%). Forest habitat on the island is characterized by loblolly pine (*Pinus taeda*; 7%) and oak (*Quercus* spp.; 1%). Open water makes up the remaining 1%. We calculated coverage of habitat types from vegetation maps developed by the National Park Service.

We captured owls at four sites in pine woods using 61-mm mist nets with broadcast of Northern Saw-whet Owl vocalizations as an audiolure (Erdman and Brinker 1997). We did not begin to capture and band until late December or early January to ensure that these owls were not migrants. We determined age by molt (Pyle 1997) and gender by DNA analysis of approximately 20 µl of blood (Fleming et al. 1996) obtained through venipuncture of a wing or leg. All owls were equipped with a 3-g backpack-harnessed transmitter representing approximately 3% of the weight of the bird. After we released the owls, we found and monitored them using a unidirectional antenna. We estimated locations by triangulation from stations with known coordinates derived from global positioning systems data. We obtained ≥3 bearings for each estimate using a hand-held receiver and yagi antenna, and we made ≤1 location/h from sunset to sunrise, following the protocol of White and Garrott (1990). We continued radiotelemetry until the birds left the island or lost their radio harness.

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We calculated home ranges for all owls (seven females) that had ≥30 accurate location estimates; two were "after hatch year" (>20 months old) and the other five were "hatch year" (8–10 months old). We overlaid location estimates on a background map of the island; any occurring outside the boundaries of the island and locations with 95% confidence ellipses with areas >500 ha were eliminated because of limited accuracy. In the final analyses, we used 871 location estimates of the 986 collected. The number of estimated locations used for an individual owl's home range calculation ranged from 36–241 and the number of days tracked ranged from 7–80. Four individuals had >100 estimated locations.

We used the fixed kernel method (Worton 1995, Seaman and Powell 1996) to calculate owl home ranges with optimal smoothing parameters chosen by least squares cross validation (LSCV). Kernel methods use a smoothing parameter "h" to smooth contours around location points. Choice of smoothing parameter by LSCV is recommended because of its objectivity, consistency of estimation, and ability to minimize the difference between true and estimated density of location points (Silverman 1986, Worton 1995, Seaman and Powell 1996). We standardized home ranges across individuals by using smoothing parameters from initial calculations for each individual to determine a median optimal smoothing parameter at 30% and 95% utilization distribution levels. Home ranges then were recalculated with the parameter set to the median value. We also calculated minimum convex polygon (MCP) home ranges for comparison with other studies.

We calculated biweekly home ranges (with smoothing parameters calculated by LSCV) for individuals tracked for >2 weeks to determine if home ranges for individuals with small numbers of location estimates accurately represented a shorter time frame (biweekly versus winter home range). This allowed us to examine whether home range size increased over time and to determine if owls with smaller data sets used areas similarly to owls that spent the winter on the island. The larger data sets were subdivided into time frames of 10–14 days. Only those biweekly data sets that included ≥25 location estimates were included in the analyses.

To calculate home range overlap, we recalculated home ranges to include only data from the time frame in which both owls were present; i.e., overlap was temporal as well as spatial. We calculated percentage overlap as twice the area of intersection divided by the total combined area of both intersecting home ranges (Churchill 1998).

We compared habitat use at owl location points with habitat available on the study area with a χ^2 goodness-of-fit test (Siegel 1956, Neu et al. 1974). To calculate habitat use, we used only those locations with 95% confidence ellipses <1 ha (an elliptical area with 95% probability of including the owl) as a compromise between sample size and accuracy of habitat identification because the probability of correctly identifying habitat increases with location precision. Fifty-four location points representing six of the seven owls used for home range analysis met this criterion. The number of points per owl ranged from 1–21 (mean = 9). Habitat availability was measured from the vegetation map of the island. Geographically contiguous habitats where owls seldom occurred and that represented small percentages of available habitat were grouped together (beach with grassland, and open water with marsh) to reduce the number of categories with <5 expected observations (Neu et al. 1974). We calculated 95% confidence intervals for each of five habitats using Bailey's confidence intervals to determine which habitats contributed significantly to the overall χ^2 statistic (Cherry 1996). Habitat availability that was higher or lower than the confidence interval for habitat use was considered significantly selected or avoided at $\alpha = 0.05$.

RESULTS

The mean 95% fixed kernel home range size was 103.5 ha (±50.3 SE) with a range of 38.5–248.6 ha (n = 7 owls). During 1996, when the wintering owl population was high, mean home range size was 61.4 ha (range = 38.5–82.1 ha, n = 4). During 1997, when the population was very low, mean home range was 159.7 ha (range = 95.9–248.6, n = 3). We were able to calculate 17 biweekly home ranges (n = 5 owls); mean biweekly 95% home range area was 112.9 ha (range = 28.6–325.9). Most of the biweekly home ranges (mean = 112.9 ha, range = 28.6–325.9) were larger than the seasonal home ranges calculated for four owls (38.5–82.1 ha). The smaller samples of these individuals resulted in home ranges that were similar to many of the biweekly home ranges but much smaller than the seasonal home ranges determined for owls with larger sample sizes.

During 1996 only one pair of individuals had overlapping home ranges (65% overlap) and during 1997 three pairs overlapped (Table 1). Representing the most overlap between any two individuals, the entire range of owl 2 was included within the range of owl 3, and the shapes of the contours were very similar.

Habitat at Northern Saw-whet Owl location points differed from habitat availability (χ^2 = 35.9, df = 4, P = 0.001); pine woods were used significantly more than expected, while marsh-open water habitats were used significantly less than expected (Table 2). We found no significant differences between expected and observed use of the other habitats.

TABLE 1. Fixed kernal home ranges of wintering Northern Saw-whet Owls (*Aegolius acadicus*) tracked on Assateague Island, Maryland, showed areas of overlap.

Dates	Owl	Home range (ha)	Overlap	
			ha	%
13 Jan. to 20 Jan., 1996	7	82.1		
	6	52.2	37.7	65.0
12 Jan. to 2 Mar., 1997	2	95.9		
	3	134.5	91.2	86.0
8 Jan. to 21 Mar., 1997	1	248.6		
	2	95.9	63.4	41.7
12 Jan. to 2 Mar., 1997	1	248.6		
	3	134.5	57.5	38.2

TABLE 2. Habitat use and availability for Northern Saw-whet Owls wintering on Assateague Island, Maryland, 1996–1997. The availability of loblolly pine habitat was less than the lower confidence limit for use of that habitat; thus, loblolly pine was used by owls significantly more than expected. Conversely, owls avoided marsh-open water habitats, as that availability was greater than the upper confidence limit for its use.

Habitat type	Habitat used (%)[a]		Habitat available (%)[c]
	Estimate	Confidence interval[b]	
Loblolly pine	52	33–69	7
Deciduous woodland	4	0–15	1
Grassland-beach	0	0–100	19
Marsh-open water	11	2–26	37
Shrub swamp	33	17–51	36

[a] Based on 54 accurate locations of six individual owls.
[b] Bailey's 95% confidence intervals for habitat (after Cherry 1996).
[c] Proportion of each habitat type on the study area based on a vegetation map developed by National Park Service.

DISCUSSION

Only three other studies have reported home range size for Northern Saw-whet Owls. All used the MCP method. Palmer (1986) estimated a breeding season home range of 78 ha based on size of the territory used by singing males. Because he did not use radio telemetry and surveyed "the optimum habitat available," this likely is a conservative estimate. The owls in our study had a somewhat larger mean winter home range than the one owl tracked by Forbes and Warner (1974) in Minnesota. The breeding season range calculated by Cannings (1987) in British Columbia (150.5 ha) was similar in size to the winter MCP range in our study (150.8 ha).

Size of winter home ranges on Assateague Island increased with time as home ranges of individuals tracked for ≥15 days were larger than biweekly home ranges. This suggests that several weeks may be needed to estimate winter home range size accurately. Consequently, we feel that the four home range estimates calculated with ≥100 location points spanning ≥15 days (mean = 137.9 ha ± 78.1 SE, range = 72.6–248.6 ha; Churchill 1998) are most representative of "winter" home ranges.

Locations of daytime roosts indicated that owls often stayed in a small area (single or multiple roosts ≤20 m from one another) for days or weeks before moving to new locations within the home range hundreds of meters away (Churchill 1998). After spending several days in the new area, owls frequently returned to their original locations. Owls returning to areas used previously, instead of exploring new areas, suggests that home range size becomes stable over time (Churchill 1998). In general, individuals that moved among several patches of conifer forest had relatively large home ranges.

The large degree of overlap in the 95% fixed kernel home ranges among individuals was expected since winter territoriality in Northern Saw-whet Owls has not been reported. If owls are opportunistic hunters, then they could be expected to move within areas of suitable habitat in search of prey. Home range overlap in general and especially the overlap and similarity in shape of the home ranges for owls 2 and 3 further suggest that this species is not territorial during winter. Similarity of home ranges also may have resulted from the habitat configuration characteristic of this portion of Assateague Island, particularly the patchy distribution of pine woods. Thirty percent home ranges usually were centered in pine woods and additional patches of pine woods often occurred at the periphery of 95% contours. Our use of median optimum bandwidth in home range calculations also may have contributed to similarity in shapes and sizes of the two 95% contours for owls 2 and 3.

Winter habitats used by Northern Saw-whet Owls are highly variable, although dense coniferous or deciduous vegetation for roosting and perches for foraging must be present (Cannings 1993). On Assateague Island, de-

ciduous forest habitat was rare, and owls inhabited loblolly pine forest or myrtle shrubland most often. Loblolly pine habitat is similar to other habitats used during winter, such as spruce-fir forests (Simpson 1972), pine groves (Swengel and Swengel 1987), pine plantings and tamarack bogs (Mumford and Zusi 1958), and pine plantations (Wilson 1938). Shrubland habitats on Assateague Island may be structurally similar to the more unusual shrub-steppe habitat described as breeding habitat by Marks and Doremus (1988) and Hayward and Garton (1984), or the hawthorne thicket reported as a wintering area by Scott (1938).

Although availability of the pine woods habitat was limited, owls used it more frequently than any other habitat type and more than expected based on availability. Presumably it contained an attractive prey base as these woods were used during nightly radio tracking when owls likely were foraging. The pine habitat also provided cover as owls frequently were located there during the day in well-hidden roosts (Churchill et al. 2000). Myrtle shrubland (the second most commonly used habitat) also was important, although its use was in proportion to availability. For example, 30% contour of owl 4 was centered in shrubland and it used shrubland extensively while spending little time in pine woods. Habitats more open than shrubland generally were avoided altogether.

Our study identified habitats within one coastal barrier island that are used by wintering Northern Saw-whet Owls. The overall importance of barrier islands as wintering habitat is still unclear. During autumn migration, more owls typically are captured at Maryland's inland banding stations than at Assateague Island, regardless of whether captures were high or low during a given year (Brinker et. al. 1997). This suggests that more owls winter in inland areas than on coastal barrier islands. Studies of the differences in quality of inland and coastal habitats would be valuable for determining if the fitness of owls wintering in the two areas differs.

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RELATIONSHIP BETWEEN HABITAT AREA AND THE DISTRIBUTION OF TIDAL MARSH BIRDS

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ABSTRACT.—To assess the relationship between marsh area and relative abundance of tidal marsh bird species, we surveyed birds on 86 circular plots in 40 salt and brackish tidal marshes in Connecticut. We measured marsh area in two ways: the amount of contiguous marsh vegetation not interrupted by broad barriers (>500 m of open water or >50 m of upland habitat) and by narrow barriers (>30 m of open water or >10 m upland). We determined the relationship between marsh area and the relative abundance of particular species (mean number of individuals per survey plot) with linear or logistic regression. When the broad barrier definition was used, we found that all three species of short grass meadow specialists, Willets (*Catoptrophorus semipalmatus*), Seaside Sparrows (*Ammodramus maritimus*), and Saltmarsh Sharp-tailed Sparrows (*A. caudacutus*), were less abundant or absent in survey plots in smaller marshes. The Seaside Sparrow and Willet also showed a significant tendency to be less frequent in smaller marshes when the narrow barrier definition was used. In contrast, species that used a wider range of wetland types, as in the Virginia Rail (*Rallus limicola*), Marsh Wren (*Cistothorus palustris*), and Swamp Sparrow (*Melospiza georgiana*), were equally frequent on plots in marshes of different areas. Our results are consistent with the hypothesis that fragmentation of marsh systems with artificial habitat causes a decline in the density of short grass meadow specialists in the remaining patches of appropriate habitat.
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Connecticut lost about 30% of its tidal wetlands between the 1880s and the 1970s (Rozsa 1995), and most of the remaining marshes have been heavily modified by ditching, tidal restriction, and the spread of common reed (*Phragmites australis*). These habitat changes are associated with population declines in salt marsh birds (Brawley et al. 1998, Benoit and Askins 1999, Clarke et al. 1984, Craig 1990), but the role of habitat fragmentation in these declines remains an open question. Species that are sensitive to the negative effects of habitat fragmentation would decline not only in areas where habitat has been altered, but also in remaining small patches of apparently suitable habitat.

Habitat fragmentation is associated with changes in the composition of bird communities in a wide range of habitats, including deciduous forests in Japan and eastern North America (Roberts and Norment 1999, Askins 2000, Askins et al. 2000), shrubsteppe in Idaho (Knick and Rotenberry 1995), temperate rain forests in Chile (Willson et al. 1994), and tropical rain forests in Brazil (Laurance et al. 2002). Some species (usually habitat specialists) in each of these habitats are area sensitive, with a tendency to decline or disappear in small remnant patches of apparently suitable habitat. However, area sensitivity has not been demonstrated conclusively in North American marsh birds despite the fact that Brown and Dinsmore (1986) and Craig and Beal (1992) showed that there was a positive relationship between the number of species of birds and marsh area, and that some species were missing from smaller marshes. The results of both of these studies were inconclusive because more time was spent surveying birds in large marshes than in small marshes. Consequently, more species may have been detected in larger marshes because of the passive sampling effect (Connor and McCoy 1979, Horn et al. 2000). Because there was less surveying effort in smaller marshes, fewer individuals would be detected, increasing the chance that some species would be missed even if none of the species were area sensitive. Moreover, neither study showed that the density of particular species of marsh birds was lower in smaller marshes than in larger marshes. In both forests (Robbins et al. 1989, Askins et al. 1990) and grasslands (Vickery et al. 1994, Johnson and Igl 2001), area sensitive species tend to have lower densities in small patches of habitat than in large blocks of continuous habitat. This may be due to negative

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edge effects such as higher predation rates in smaller patches (Johnson and Temple 1990, Faaborg et al. 1995).

We especially focused on two species of sparrows that are salt marsh specialists, the Seaside Sparrow (*Ammodramus maritimus*) and Saltmarsh Sharp-tailed Sparrow (*A. caudacutus*), because they are taxonomically and ecologically similar to area sensitive sparrows of dry grasslands. Moreover, in New England the two salt marsh sparrows are largely restricted to short grass meadows, salt and brackish tidal wetlands dominated by low grasses such as *Spartina patens*, *Distichlis spicata*, and *Juncus gerardi* (Greenlaw and Rising 1994, Post and Greenlaw 1994, Benoit and Askins 1999). In many respects, these habitats are structurally similar to upland grasslands. Studies in dry grasslands such as prairie preserves in Illinois (Herkert 1994a), blueberry barrens in Maine (Vickery et al. 1994), fields in western New York (Norment et al. 1999), and restored grasslands in the northern Great Plains (Johnson and Igl 2001) showed that Vesper Sparrows (*Pooecetes gramineus*), Savannah Sparrows (*Passerculus sandwichensis*), Grasshopper Sparrows (*Ammodramus savannarum*), Baird's Sparrows (*A. bairdii*), and Henslow's Sparrows (*A. henslowii*) were more likely to be detected on standard plots in large grasslands than in plots of the same size in small grasslands. Moreover, these species tend to be missing in survey plots located in the smallest grasslands. Consequently, an important concern in managing or restoring grasslands is to provide large enough areas of contiguous habitat to support populations of these sparrows. Similarly, if the salt marsh sparrows are area sensitive, then it will not be sufficient to consider the total amount of suitable habitat needed to support populations; it also will be important to maintain or create large blocks of uninterrupted short grass meadow.

Our goal was to determine whether specialized marsh birds are area sensitive. If they are, then we would expect them to display either of the following patterns: (1) a lower density in smaller marshes, or (2) a tendency to be absent from survey plots in marshes smaller than some minimum area. We completed surveys in a large number of tidal marshes to test these predictions.

METHODS

Survey plots.—During the summers of 1995 and 1996, we surveyed birds and vegetation on 86 standardized circular plots in 40 brackish and salt marshes along the coast and tidal rivers of Connecticut (see Benoit and Askins 1999 for locations and descriptions of these sites, including the number of survey plots per site). We surveyed 20 marshes during each of the two years. These encompassed nearly all salt and brackish marshes >10 ha in the state as well as some marshes <10 ha. The 50-m radius plots were located ≥200 m apart and ≥75 m from upland habitats. We recorded all birds detected during an observation period during each of two visits, one in June and the other (≥2 weeks later) in July. We commenced the study in early June because Seaside and Saltmarsh Sharp-tailed sparrows are still migrating during late May (Saunders 1959). We conducted observations between 05:00 and 10:00 EST, and we surveyed ≤4 plots per day. The observation period consisted of 10 min of passive observation followed by 7 min of broadcasting, in sequence, the taped calls of the following species: Least Bittern (*Ixobrychus exilis*), American Bittern (*Botaurus lentiginosus*), Virginia Rail (*Rallus limicola*), King Rail (*R. elegans*), Clapper Rail (*R. longirostris*), Sora (*Porzana carolina*), and Black Rail (*Laterallus jamaicensis*). Playback was not necessary for highly detectable birds such as sparrows, Willets (*Catoptrophorus semipalmatus*), and Marsh Wrens (*Cistothorus palustris*). We quantified the relative abundance of each species as the total number of individuals seen or heard during the initial 10 min plus any additional birds that responded to conspecific calls during the playback period. We counted only the adults of each species. Individuals of the same species had to be detected simultaneously to be recorded as different individuals. These survey methods were appropriate for sampling bird distribution across a regional landscape and were not intended to characterize particular marshes.

We chose survey plots by stratified random design. We mapped major vegetation types using aerial photographs supplemented with field checking. We initially classified vegetation into three categories (Table 1): (1) short grass meadow (areas dominated by low marsh grasses such as *Spartina patens*, *Juncus gerardi*, and *Distichlis spicata*), (2) cattail (areas dominated by *Typha* spp.), and (3) *Phragmites* (areas dominated by *Phragmites australis*). We used a table of random numbers to select coordinates of survey plots in each sufficiently extensive vegetation type on a grid superimposed on a map of each site. Each marsh had 1–5 survey plots, depending upon its size.

We used the line intercept method (Brower and Zar 1977) to estimate percent cover of different species of plants on each plot. Two 50-m perpendicular transects were laid out from the center of each plot. One of the transects was oriented toward the nearest tidal creek. We calculated percent cover from the total distance that the line intercepted the foliage of each plant species. Based on the dominant vegetation indicated by

TABLE 1. Mean percent cover for different plant species and water features for six vegetation categories in 40 tidal marshes on the coast of Connecticut, 1995–1996.

	Vegetation categories					
	Short grass meadow	*Phragmites*	Cattail	Brackish mixture	Short *S. alterniflora*	Other
No. of survey plots	36	14	7	14	6	9
Cover types						
Tall *S. alterniflora*	7 ± 10[a]	1 ± 4	0 ± 0	5 ± 12	9 ± 5	23 ± 32
Short *S. alterniflora*	10 ± 12	0 ± 0	0 ± 0	0 ± 0	58 ± 9	0 ± 0
Spartina patens	33 ± 19	4 ± 8	0 ± 0	15 ± 12	7 ± 11	0 ± 1
Juncus girardi	16 ± 20	1 ± 3	0 ± 1	11 ± 12	0 ± 0	3 ± 8
Distichlis spicata	10 ± 12	1 ± 3	0 ± 0	2 ± 6	0 ± 0	0 ± 0
Phragmites australis	1 ± 2	73 ± 13	15 ± 12	21 ± 15	0 ± 0	16 ± 22
Typha angustifolia	0 ± 0	3 ± 6	53 ± 15	7 ± 11	0 ± 0	13 ± 19
Forbs	4 ± 6	1 ± 2	4 ± 4	5 ± 6	0 ± 0	6 ± 9
Scirpus spp.	0 ± 0	1 ± 2	5 ± 12	15 ± 15	0 ± 0	5 ± 12
River	5 ± 10	2 ± 5	4 ± 7	6 ± 10	4 ± 10	0 ± 0
Mosquito ditch	1 ± 1	0 ± 1	0 ± 0	0 ± 1	2 ± 1	0 ± 1
Pool	1 ± 3	2 ± 4	2 ± 2	2 ± 4	0 ± 0	2 ± 4
Creek	3 ± 6	7 ± 11	6 ± 10	1 ± 2	14 ± 12	9 ± 15

[a] Mean (± SD) percent cover for all vegetation plots.

these percent cover values, we classified each survey plot into one of the following categories: short grass meadow, cattail, *Phragmites*, short *Spartina alterniflora*, or brackish mixture (areas of short grass intermixed with patches of tall plants such as *Phragmites*, *Typha*, or *Scirpus*; Benoit and Askins 1999; Table 1). The proportion of plots in each marsh with a particular vegetation type was used as a measure of proportion of the marsh covered by that vegetation. Because of the stratified random selection of plots, this measure emphasized any large scale heterogeneity in vegetation types within the marsh.

Marsh area and birds.—We used either linear or logistic regression to determine the relationship between marsh area and the abundance of species that nest primarily in marshes. We determined the total area of each marsh complex by using a geographical information system with hydrology maps downloaded from the Univ. of Connecticut Map Library web site, http://magic.lib.uconn.edu. For this analysis, we defined marsh area as any marshlands connected by tidal flow, where marsh patches were separated by broad barriers of <500 m of open water or <50 m of uplands. The marsh area of small tributaries was included only up to a distance of 500 m from the main river.

For regression analyses, we used data from survey plots only if the plot had the appropriate vegetation for the bird species in question, as determined by the results from multiple regression analysis (Benoit and Askins 1999), and from previously published findings on habitat requirements. We used data from short grass meadow plots for analysis of Willets, Seaside Sparrows, and Saltmarsh Sharp-tailed Sparrows, while data from *Phragmites*, cattail and brackish mixture plots were used for Marsh Wrens and Swamp Sparrows. We used data from cattail and brackish mixture plots for analysis of Virginia Rails. If more than one survey plot in the same marsh complex had appropriate vegetation, then we used the mean number of individuals for these survey plots as a measure of the density of a species in the marsh.

We used linear regression to assess the relationship between marsh area and density for the following species of marsh specialists: Willets, Marsh Wrens, and Saltmarsh Sharp-tailed Sparrows. Linear regression analysis was not appropriate for species with a large number of plots with zero values, so we used logistic regression. In some of the regressions for Willets and Seaside Sparrows it was not possible to use logistic regression because of a dichotomous pattern in which a species was absent at all sites smaller than a threshold area and present at all sites larger than that area. In these cases we used the logistic transformation to normalize abundance and then used linear regression analysis. When regression results were not significant, we assessed the power of the tests by calculating the power for the correlation coefficients for the same data, as recommended by Zar (1999).

We also used the following equation developed by Simberloff and Gotelli (1984) to determine the probability that the minimum habitat area occupied by a particular species is larger than one would expect based on chance:

$$P = \frac{\binom{(S - L_i + 1)}{N_i}}{\binom{S}{N_i}}$$

where P is the probability that a smaller marsh would not be occupied if the distribution were random. S is

TABLE 2. Relationship between the relative abundance (mean number of individuals per survey plot) and habitat area using the "broad barrier" criterion[a] for three species of salt marsh specialists and three generalist marsh species in tidal marshes on the coast of Connecticut that were surveyed in June and July, 1995–1996.

	Linear regression[b]			Logistic regression[b,c]		Minimum area (ha)[d]	Simberloff-Gotelli test
	F	df	*P*	Wald χ^2	*P*		*P*
Salt marsh specialists							
Willet	17.5[e]	1, 17	0.001			138	0.009
Saltmarsh Sharp-tailed Sparrow	5.7	1, 17	0.029			10	0.263
Seaside Sparrow				5.0	0.03	67	0.001
Marsh generalists							
Virginia Rail				1.03	0.31	80	0.357
Marsh Wren	2.1	1, 12	0.173			8	1.000
Swamp Sparrow				3.45	0.63	55	0.070

[a] Separate marshes were defined by barriers of >500 m of open water or >50 m of upland.

[b] We used the ln transformation to normalize the distribution of habitat area for all regression analyses.

[c] Distributions were analyzed with linear regression analyses except for species with a large number of plots with zero values, in which case we used logistic regression analyses.

[d] Area of smallest marsh at which a species was detected.

[e] It was not possible to calculate an equation with logistic regression for this species because of the dichotomous pattern, with Willets absent at all sites <138 ha and present at all sites ≥138 ha. We therefore used the logistic transformation to normalize Willet abundance (y): new y = ln((1.6 − (y + 0.01))/(y + 0.01)). We then completed a linear regression analysis.

the number of sites, N_i is the number of sites where species i occurs, and L_i is the size rank of the smallest site occupied by species i. As in the regression analyses, we used only those plots with suitable habitat for each species. Only one randomly chosen plot was used for each marsh so that the samples would be independent. This is a conservative test of area sensitivity because the key variable is the rank of the smallest site even in cases in which the smallest site is substantially smaller than the median or mean area of sites occupied by the species.

We defined the boundaries separating different marshes more conservatively, with narrower barriers, in a second set of regression and Simberloff-Gotelli analyses. In this case, boundaries of a marsh were delimited by the smallest barriers one can see in the field or on an aerial photograph: (1) any body of water >30 m wide at its narrowest point, (2) roads or railroad tracks, or (3) ≥10 m of adjacent uplands (as designated by the hydrology maps). In this way, we could determine whether narrow interruptions in marsh habitat were related to bird distributions.

To ensure that any relationship between bird abundance and marsh area were not due to a confounding variable, we also completed multiple regression analyses for all species that showed a significant relationship with marsh area. The dependent variable was the mean number of individuals per plot and the independent variables were marsh area (as defined by broad barriers), the proportion of the entire marsh that had appropriate vegetation for a particular species, and the mean percent cover of pools, creeks, and ditches in the marsh. Previous studies have shown that the percent cover of water features is an important predictor of the distribution of marsh birds (Craig and Beal 1992, Reinert and Mello 1995, Benoit and Askins 1999). Only those survey plots with suitable habitat for a particular species were included in the analysis, which helped to control for relationships with vegetation structure and composition.

RESULTS

Using linear regression, and the broader definition of marsh area (in which marshes must be separated by wide barriers to be considered separate), we found that the density of both Willets and Sharp-tailed Sparrows exhibited a positive relationship with marsh area (Table 2, Fig. 1). In contrast, Marsh Wrens were not area dependent (Table 2, Fig. 2). The statistical power for the correlation between ln marsh area and density of Marsh Wrens was 0.73, indicating that there was a 27% chance of a type II error.

We used logistic regression to analyze the distributions of Virginia Rails, Swamp Sparrows (*Melospiza georgiana*), and Seaside Sparrows because these species were absent from a large proportion of the plots and consequently did not have normal distributions. When we used the broad barrier definition of marsh area, there was a significant positive relationship between frequency of occurrence and marsh area for Seaside Sparrows, but not for Virginia Rails or Swamp Sparrows (Table 2, Figs. 1 and 2). The statistical power for the latter two species was 0.85 and 0.72, respectively.

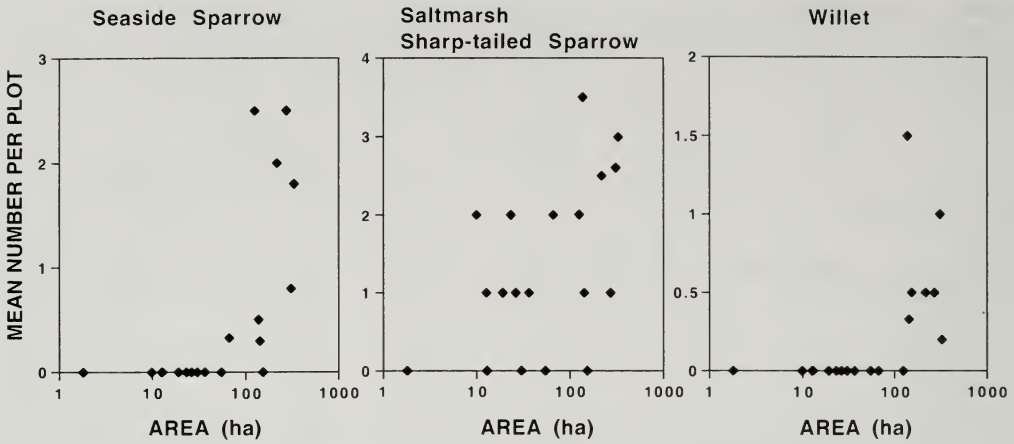

FIG. 1. The densities of salt marsh specialists were positively related to the size of the marsh. Data were collected from 50-m radius plots in short grass meadow habitat of tidal marshes along the Connecticut coast, 1995–1996. Marshes separated by >500 m of open water or >50 m of upland habitat ("broad barrier" criteria; see text) were considered distinct.

Using the narrow barrier definition of marsh area (in which small patches of marsh vegetation separated by narrow barriers were considered as separate marshes) in regression analyses, we found that only the Willet and Seaside Sparrow were significantly less frequent in smaller marshes than in larger marshes (Table 3). The statistical power for species that did not show significant relationships with marsh area was 0.56 for Saltmarsh Sharp-tailed Sparrow, 0.97 for Swamp Sparrow, 0.99 for Marsh Wren and 0.94 for Virginia Rail.

Using the Simberloff-Gotelli equation with data for the broad barrier definition of marsh area, we found that the smallest marsh where a species was detected was larger than expected by chance for Seaside Sparrows and Willets, but not for Saltmarsh Sharp-tailed Sparrows or the more generalist marsh species (Table 2). Using the narrow barrier definition of marsh area, only the Seaside Sparrow had

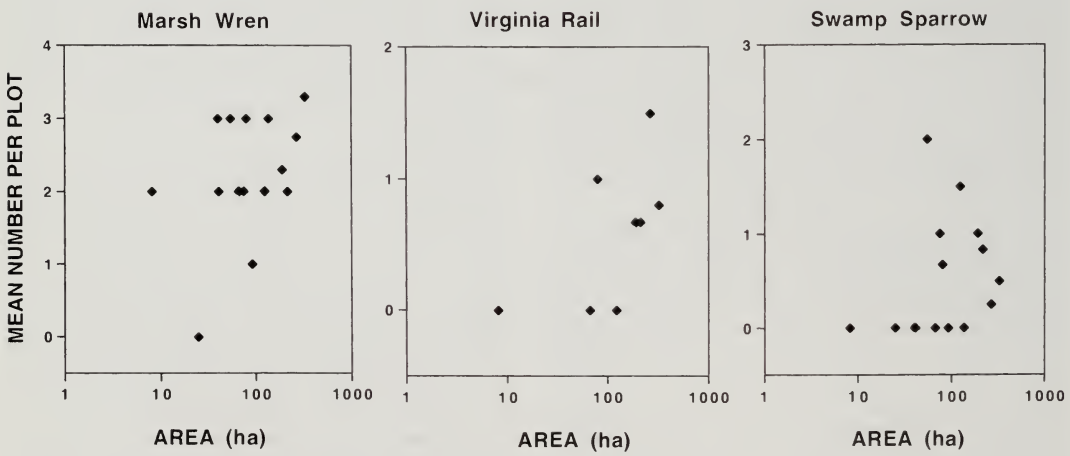

FIG. 2. The densities of generalist marsh species were not related to the size of the marsh. Data were collected from 50-m radius plots in tall grass meadow habitats of tidal marshes along the Connecticut coast, 1995–1996. Marshes separated by >500 m of open water or >50 m of upland habitat ("broad barrier" criteria; see text) were considered distinct.

TABLE 3. Relationship between the relative abundance (mean number of individuals per survey point) and habitat area using the "narrow barrier" criterion[a] for three species of salt marsh specialists and three generalist marsh species in tidal marshes on the coast of Connecticut that were surveyed in June and July, 1995–1996.

	Linear regression[b]			Logistic regression[b,c]		Minimum area (ha)[d]	Simberloff-Gotelli test
	F	df	*P*	Wald χ^2	*P*		*P*
Salt marsh specialists							
Willet				4.5	0.03	16	0.081
Saltmarsh Sharp-tailed Sparrow	3.6	1, 24	0.07			4	0.231
Seaside Sparrow				4.1	0.04	15	0.048
Marsh generalists							
Virginia Rail				0.01	0.91	10	0.429
Marsh Wren	0.1	1, 22	0.73			4	1.000
Swamp Sparrow				0.07	0.93	8	0.217

[a] Separate marshes were defined by barriers of >30 m of open water or >10 m of upland.
[b] We used the ln transformation to normalize the distribution of habitat area for all regression analyses.
[c] Distributions were analyzed with linear regression analyses except for species with a large number of plots with zero values, in which case we used logistic regression analyses.
[d] Area of smallest marsh at which a species was detected.

a minimum area significantly larger than expected by chance (Table 3).

Multiple regression analysis indicated that marsh area was the best predictor of the mean number of individuals per plot for each of three short grass meadow specialists (Willet, Saltmarsh Sharp-tailed Sparrow, and Seaside Sparrow; Table 4). The two other independent variables, percentage of the entire marsh covered with short grass meadow and percent cover of pools, ditches and creeks, were not significantly related to abundance for any of these species. The overall model for the Saltmarsh Sharp-tailed Sparrow was not significant ($P = 0.083$), but marsh area tended to explain more variation than the other two variables (Table 4).

DISCUSSION

Although area dependent relationships have been shown for many species of grassland birds (Herkert 1994a, Vickery et al. 1994, Johnson and Igl 2001), this study is the first to conclusively demonstrate such a relationship for salt marsh sparrows. Both species of sparrows that are associated with short grass meadows were more frequent in plots in larger marshes than in similar plots in smaller marshes, and marsh area was a better predictor of the density of these species than the per-

TABLE 4. Multiple regression analysis with mean number of individuals per survey plot as the dependent variable and marsh area, percent of marsh covered with short grass meadow, and percent cover of small water features (pools, creeks, and ditches) as independent variables. Data are from surveys of tidal marshes on the coast of Connecticut, 1995–1996.

	Model		Marsh area[a,b]			Percent short grass meadow[b,c]			Percent water[b,d]		
Species	*F*	*P*	*t*	*P*	Trend	*t*	*P*	Trend	*t*	*P*	Trend
Willet[e]	10.1	0.001	5.4	0.0002	+	0.1	0.92		1.4	0.19	
Saltmarsh Sharp-tailed Sparrow	2.8	0.083	2.4	0.0342	+	1.0	0.32		1.0	0.32	
Seaside Sparrow[f]	8.7	0.002	5.1	0.0003	+	0.1	0.92		0.0	0.97	

[a] Separate marshes were defined by the broad barrier criterion (separation by >500 m of open water or >50 m of upland).
[b] To normalize distributions, we used the ln transformation for marsh area and percent cover water, and the arcsine transformation for percent short grass meadow.
[c] Percent of marsh surface covered with short grass meadow.
[d] Percent of marsh surface covered with creeks, ditches, and pools.
[e] We used the logistic transformation to normalize Willet abundance (y): new y = ln((1.6 − (y + 0.01))/(y + 0.01)). We then completed a linear regression analysis.
[f] We used the logistic transformation to normalize Seaside Sparrow abundance (y): new y = ln((2.6 − (y + 0.01))/(y + 0.01)). We then completed a linear regression analysis.

centage of the site covered with short grass meadow or with pools and other water features. Although Saltmarsh Sharp-tailed Sparrows were detected in some of the smallest marshes, they exhibited a significant positive relationship with marsh area. The Seaside Sparrow, which had a lower overall abundance than the Sharp-tailed Sparrow (Benoit and Askins 1999), was restricted to the largest marshes. The mean size of Seaside Sparrow territories in ditched marshes was <1 ha (Marshall and Reinert 1990), which is not large enough to explain their absence in marshes smaller than 67 ha (Table 2). Saltmarsh Sharp-tailed Sparrows are not territorial and have small home ranges (1.2–5.7 ha for males and smaller for females; Woolfenden 1956, Greenlaw 1993, Greenlaw and Rising 1994) so, as in the Seaside Sparrow, this species is more frequent in larger marshes for some reason other than minimum area requirements for territories or home ranges. Perhaps larger marshes have lower rates of nest predation (Johnson and Temple 1990) or a better food supply (Burke and Nol 1998).

Willets are another short grass meadow species that appear to be area sensitive. Marsh area was a better predictor of their abundance than percent cover of short grass meadow or of water features, and they were absent in marshes <138 ha (Table 2). This species was more abundant during the 19th Century, but hunting and egg collecting probably contributed to its extirpation from Connecticut's marshes (Bevier 1994). After an absence of nearly 100 years from the state, it has recolonized a handful of salt marshes (Craig 1990). The current association of Willets with large marshes may indicate that the few individuals present have their choice of the best habitat, which probably are the largest marshes with abundant nesting and feeding sites. Although nesting attempts have been detected at smaller marshes (Bevier 1994), Willets often nest in high density clumps to enhance synchronous nesting and increase predator-mobbing effectiveness (Burger and Shisler 1978, Howe 1982), so it is likely that birds establishing new breeding territories will join the existing nesting populations on the large sites.

Even though the minimum habitat areas listed for Seaside Sparrows and Willets (Table 2) are significantly larger than expected by chance, these values should not be interpreted as the smallest habitat areas that can accommodate these species. They merely reflect the minimum areas for our sample of 40 marshes. The distribution of these species indicates that they tend to be absent from small marshes.

In contrast to the short grass meadow specialists, two species associated with cattail marsh and *Phragmites*, the Marsh Wren and Swamp Sparrow, did not show a significant relationship with marsh area. Statistical power was great enough in these analyses (>0.7 for the "broad barrier" data and >0.9 for the "narrow" barrier data) that we can be reasonably confident that a substantial relationship does not exist. Herkert (1994b) found that in Illinois prairies certain grassland birds were area sensitive while other species responded only to the structure of the vegetation. This also may be the case with tidal marsh birds. Marsh Wrens and Swamp Sparrows appear to respond to plant structure because they are found in many different types and sizes of wetlands as long as there is tall, sturdy vegetation for their nests (Kroodsma and Verner 1997, Mowbray 1997, Benoit and Askins 1999).

The Virginia Rail also nests in a wide variety of marsh types and it, too, may choose nest sites based primarily on the structure of the vegetation (Conway 1995). We recorded Virginia Rails only in relatively large marshes (Fig. 2), but the relationship between the occurrence of this species and marsh area was not significant. This may have been due to our small sample size, but the power of this test was relatively high (0.72). In a survey of water birds in numerous wetlands in Maine, Gibbs et al. (1991) reported a moderately higher frequency of Virginia Rails in larger marshes than in smaller marshes, but this may merely reflect greater sampling effort in larger marshes. Even though Brown and Dinsmore (1986) sampled more plots in large marshes than in small marshes, they found that Virginia Rails were equally frequent in marshes of different areas. If Virginia Rail frequency increases with habitat area, the relationship does not appear to be strong.

Short grass meadow specialists may be especially sensitive to habitat destruction or degradation because of their association with large marshes. Many specialized grassland

birds also are area sensitive, and the increasing fragmentation of prairies and other grasslands has been linked to the decline of these species (Herkert 1994a, 1994b; Vickery et al. 1994). Tidal marshes, which may be considered a type of grassland, also have been subject to fragmentation (Niering and Bowers 1966, Bongiorno et al. 1984). Human activities that dissect salt marshes or otherwise reduce their total area may contribute to the decline of short grass meadow specialists. Furthermore, the replacement of short graminoids by *Phragmites* may reduce already limited habitat for these species (Benoit and Askins 1999). Marshes where tidal flow has been restricted by tide gates, dikes, or road construction are especially susceptible to invasion by *Phragmites* (Bongiorno et al. 1984, Roman et al. 1984, Sinicrope et al. 1990). These sites should have high priority for restoration in order to re-establish large expanses of short grass vegetation.

Our results are consistent with the hypothesis that fragmentation of continuous short grass marshes with artificial barriers will not only directly destroy marsh habitat, but also will have a negative effect on the abundance of short grass meadow specialists in the remaining patches of undisturbed habitat. This may apply especially to Seaside Sparrows and Willets, which showed a positive correlation with marsh area even when marshes were considered distinct if they were separated by only 10 m of upland habitat or 30 m of open water. The abundance of more generalist marsh species, including those associated with cattail and *Phragmites*, appears to be less sensitive to habitat fragmentation.

Neither the broad barriers nor the narrow barriers that we used to delineate marshes in separate analyses are likely to inhibit the dispersal of marsh bird species, many of which migrate across great distances. It is more likely that these barriers serve as indicators of habitat edge. In forests and grasslands negative edge effects such as increased rates of nest predation and brood parasitism account for the low density of some species of birds in small habitat patches (Faaborg et al. 1995). Our goal was to determine whether the major edges associated with broad barriers (such as extensive residential areas or forest) and the minor edges associated with narrow barriers (such as railroad tracks and roads) are associated with the occurrence and density of marsh bird species. Our results suggest that both types of edges may be related to the distribution of bird species that are found primarily in short grass meadows. Research on the nest success and survivorship of these species is needed, however, to determine if there is a selective advantage to avoiding smaller marshes.

Marshes can be managed for salt marsh birds by protecting entire marsh systems from development to prevent reduction of the total area of contiguous habitat and by not constructing canals, causeways, and other artificial barriers that divide a large marsh into smaller patches. Where such structures already have been built, marshes can be restored by removing them. Large, continuous marsh systems dominated by short grass meadows should have a high priority for protection and, if necessary, restoration to sustain specialized species of marsh birds.

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AVIAN COMMUNITY RESPONSE TO SOUTHERN PINE ECOSYSTEM RESTORATION FOR RED-COCKADED WOODPECKERS

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ABSTRACT.—The effects of Red-cockaded Woodpecker (*Picoides borealis*) management on nontarget birds is not widely known. Intensive management for pine specialists such as the Red-cockaded Woodpecker may negatively impact both Nearctic-Neotropical and Temperate Zone migrants associated with hardwood vegetation. To evaluate possible positive and negative associations, we surveyed avian communities from 1995–1997 using point counts within managed Red-cockaded Woodpecker cavity tree clusters and mature forest control sites in longleaf pine (*Pinus palustris*) and loblolly (*P. taeda*)-shortleaf (*P. echinata*) pine habitats. In general, sites managed for Red-cockaded Woodpeckers supported more diverse and numerous bird populations than mature forest control sites. During the breeding season in loblolly-shortleaf and longleaf pine habitats, respectively, species richness was 47% and 23% greater, avian abundance was 57% and 65% greater, and bird species diversity was 25% and 21% greater within managed Red-cockaded Woodpecker cluster sites than within control sites. During winter, species richness and avian abundance each were 52% higher within managed Red-cockaded Woodpecker cluster sites than control sites in loblolly-shortleaf pine habitat. *Received 30 January 2002, accepted 12 August 2002.*

Studies in Texas and across the southeastern United States have indicated that many Red-cockaded Woodpecker (*Picoides borealis*) populations on national forest lands declined during the 1980s (Conner and Rudolph 1989, Costa and Escano 1989) and 1990s (U.S. Dept. of Agriculture 1995), although a few have increased (Hooper et al. 1991, Richardson and Stockie 1995). In an effort to stabilize and recover populations of this endangered woodpecker, the U.S. Forest Service initiated habitat management to restore southern pine ecosystems and provide vegetative and landscape conditions more suitable for the woodpecker on national forests throughout the southeastern United States (U.S. Dept. of Agriculture 1995). An integral part of this new management direction is the restoration of pine ecosystems with a grass-forb herbaceous layer and reduction of hardwood mid- and understory vegetation within Red-cockaded Woodpecker habitat management areas through mechanical removal of encroaching hardwood midstory and an aggressive prescribed fire program.

The Red-cockaded Woodpecker is a cooperatively breeding species indigenous to the southeastern United States (Conner et al. 2001). Young woodpeckers, typically males from previous broods, often remain with the breeding pair and assist in subsequent nesting efforts by feeding and incubating young, excavating cavities, and helping to defend the group's territory (Ligon 1970, Lennartz et al. 1987, Walters et al. 1988, Conner et al. 2001). An aggregation of cavity trees, termed the cavity tree cluster, is defended by a group of woodpeckers.

Throughout the eastern and western United States, populations of many species of Nearctic-Neotropical migrant birds appear to be suffering long term declines (Whitcomb et al. 1981, Ambuel and Temple 1983, Robbins et al. 1989). Declines of some Nearctic-Neotropical migratory birds may be related to increased nest predation and Brown-headed Cowbird (*Molothrus ater*) nest parasitism (Gates and Gysel 1978, Whitcomb et al. 1981, Wilcove 1985, Small and Hunter 1988, Terborgh 1989). Extensive opening and thinning of the forest associated with Red-cockaded Woodpecker management could increase the apparent edge as perceived by Brown-headed Cowbirds. Nest parasitism and predation rates

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appear to be greater in edge habitats than in forest interiors (Gates and Gysel 1978, Temple and Cary 1988).

Concern over declining populations of many Nearctic-Neotropical migrant birds recently has intensified and programs to determine causes and reverse declines have been sought (Keast and Morton 1980, Hagan and Johnston 1992, Finch and Stangel 1993). Effects of Red-cockaded Woodpecker management on sensitive species such as Bachman's (*Aimophila aestivalis*) and Henslow's (*Ammodramus henslowii*) sparrows and Southeastern American Kestrels (*Falco sparverius paulus*) are of concern to managers. Hunter et al. (1994) predicted that management for Red-cockaded Woodpeckers and other southern pine specialists would benefit these generally rare species. They also concluded that management that promotes hardwoods within longleaf (*Pinus palustris*) and loblolly (*P. taeda*)-shortleaf (*P. echinata*) pine stands is largely detrimental to pine specialists and provides little benefit to Nearctic-Neotropical migrants associated with hardwood forests. Many Nearctic-Neotropical migrants are known to be positively associated with hardwood mid- and understory foliage (Conner and Adkisson 1975; Conner et al. 1979, 1983; Dickson et al. 1993a). Removal or reduction of these components of forest structure has the potential to greatly reduce species that depend upon hardwood foliage for nesting and foraging in both the mid- and understory layers.

Alternatively, restoration of an open grass-forb herbaceous layer may provide suitable habitat for increases of avian species that have been reduced in numbers by past exclusion of fire, such as the Northern Bobwhite (*Colinus virginianus*; Brennan 1991). Bowman et al. (1999) noted numerous benefits of Red-cockaded Woodpecker management for some game species; white-tailed deer (*Odocoileus virginianus*) benefited from increased forage production, Wild Turkey (*Meleagris gallopavo*) hens benefited from improved nesting habitat and increased soft mast production, and Northern Bobwhites benefited from increases in herbaceous ground cover, arthropods, and native legumes, which improved nesting and foraging habitat quality.

The relationships between management of woodpecker clusters and both Nearctic-Neotropical migrants and resident bird populations are not precisely known. Preliminary results from a one-season study in loblolly pine habitat in Mississippi during winter suggest that avian species richness and abundance were greater in managed woodpecker clusters than in control areas (Brennan et al. 1995). Wilson et al. (1995) indicated that some ground-nesting birds in shortleaf pine forests in Arkansas were more abundant in untreated forest than in sites thinned and burned for Red-cockaded Woodpeckers. However, restoration of shortleaf pine-grassland communities appeared to favor some Nearctic-Neotropical migrants such as Eastern Wood-Pewees (*Contopus virens*) and Prairie Warblers (*Dendroica discolor*). Plentovich et al. (1998) suggested that management for Red-cockaded Woodpeckers enhances Bachman's Sparrow habitat. Based on an analysis of information synthesized from the literature, Hunter et al. (1994) speculated that Red-cockaded Woodpecker management might have a negative stand level impact on some Nearctic-Neotropical migrants, but such problems would likely not operate at a larger landscape scale. Breeding Bird Surveys indicated that 86 species of birds (excluding Nearctic-Neotropical migrants) are known to use longleaf pine forests where management regimes of selective harvesting and growing season fire closely resemble Red-cockaded Woodpecker management (Engstrom 1993).

Because limited information was available on the relationships between Red-cockaded Woodpecker management and avian communities in both loblolly-shortleaf pine and longleaf pine habitats, we examined species presence and relative abundance in both pine habitat types during spring and winter over a 3-year period. We also examined vegetation characteristics potentially associated with differences among bird communities. In addition to avian community level relationships, we explored both the positive and negative associations of management with Nearctic-Neotropical migrants, year round residents, and winter residents.

METHODS

We surveyed avian communities using point, time-area counts (Reynolds et al. 1980) during the spring (1 May through 15 June) and winter (1 January

through 15 February) seasons of 1995, 1996, and 1997. We surveyed birds in 20 Red-cockaded Woodpecker cavity tree clusters where management had been implemented recently and in 20 control areas within 800 m of woodpecker clusters where no additional management was implemented and hardwood midstory was present. We randomly selected control areas by using a hand held spinner to determine a direction to walk from the center of the woodpecker cluster area. If an appropriate mature forest stand of similar tree height to the cluster was not found within 800 m, a new random direction was selected. Within all 20 cavity tree clusters, all hardwoods <20 m from cavity trees had been removed, all midstory and understory hardwoods within the entire cluster area had been mulched, and the clusters had been thinned (overstory pines were removed) and prescribed burned within the past five years. Further management in cluster areas and control sites was not conducted during the study. We evaluated woodpecker cavity tree clusters in both longleaf pine and loblolly-shortleaf pine habitats. Longleaf pine study areas for woodpecker clusters and surrounding habitat were located in eastern Texas on the southern portion of the Angelina National Forest (31° 15′ N, 94° 15′ W) and loblolly-shortleaf pine study areas were located on the northern portion of that forest.

We established avian census points for time-area counts in woodpecker clusters in the geometric center of cluster areas and at randomly determined points in control areas. We selected census points in control areas by walking 100 m into the stand during our walk from cluster areas. We counted birds weekly at each census point, six times per season (Reynolds et al. 1980), and we calculated a mean abundance value for each species at each point per season per year for subsequent analyses. Two observers surveyed all points on each census day with each observer surveying 10 treatment and 10 control points per day. Bird detections were recorded upon entrance into the 50-m radius around the census point to account for birds that may flush and leave the area and all birds observed or heard within the circular plot were recorded for a total of 5 min (Hutto et al. 1986). Birds flying above the forest canopy were not counted. Surveys began at sunrise and ended <3 h later. We did not survey birds during heavy or moderate rain or high wind (>19 kph), but did survey during mist and light drizzle (Conner and Dickson 1980).

We measured forest structure and tree species composition within cavity tree clusters and control areas. We established an 11.2-m radius plot at each census point and measured vegetation height, tree density and basal area of over- and midstory trees, canopy closure, and horizontal foliage density (MacArthur and MacArthur 1961) at 1, 2, and 3 m. We estimated grasses and dicotyledonous/fern ground cover using a 4-cm diameter tube held vertically (James and Shugart 1970).

We used a Kolmogorov-Smirnov test to evaluate the distribution of data by season and treatment (SAS Institute, Inc. 1988). Data deviated slightly from normality ($0.049 > P > 0.046$) in a few instances. Because skewness and kurtosis were not a problem, we used parametric analyses to evaluate data as suggested by Sokal and Rohlf (1969:377). We used two-way analysis of variance (year × treatment) to compare avian species richness, equitability, and abundance among treatments during spring and winter ($\alpha = 0.05$). We also compared avian abundance for species detected during spring and winter among habitat treatments using two-way analysis of variance (year × treatment). We examined variation in forest structure and vegetation characteristics among treatments with a one-way analysis of variance. We used Duncan's Multiple Range Test to evaluate specific differences among treatments because sample size among treatments was equal. We included 22 species of rarely detected birds (<10 individuals detected at all points) in calculations of species richness and equitability, but excluded them from analyses beyond the community level because of their low detection rate.

RESULTS

Red-cockaded Woodpecker management restored vegetation structure to a more open park-like condition (Table 1). Hardwood basal area was 97% less in woodpecker cluster areas than in mature forest control sites. Hardwood midstory, as measured by hardwood stem density, also tended to be less (88–100%) in woodpecker cluster areas than in control sites. In response to a more open canopy, the absence of a hardwood midstory layer, and soil disturbance in cluster areas, woody shrub layer vegetation was 20–140% more abundant in cluster areas than in control sites. The openness created by the removal of hardwood midstory also was associated with a 200–300% increase in the grass component and concurrent 57–63% decrease in the fern and dicotyledonous component of the ground cover, suggesting the initial success of management in restoring woodpecker clusters to an open pine ecosystem.

Sites managed for Red-cockaded Woodpeckers generally supported more abundant and species rich bird populations than mature forest control sites (Table 2). During spring, species richness and avian abundance were greater within managed Red-cockaded Woodpecker cavity tree cluster sites in loblolly-shortleaf (23, 57, and 25% greater, respectively) and longleaf pine habitats (47, 65, and 21% greater, respectively) than in their respective mature forest control sites. Species richness and avian abundance each were 52%

TABLE 1. Forest vegetation characteristics measured at bird census point-count sites in Red-cockaded Woodpecker (*Picoides borealis*, RCW) cavity tree clusters and noncluster control sites in loblolly-shortleaf pine and longleaf pine forest types during 1995 on the Angelina National Forest in eastern Texas ($n = 10$ for each treatment). Values are means (SD). Within each row, values with the same letter are not significantly different ($P > 0.05$, one-way ANOVA with Duncan's Multiple Range Test).

Vegetation characteristic	Habitat treatment			
	Loblolly-shortleaf pine RCW cluster	Loblolly-shortleaf pine control	Longleaf pine RCW cluster	Longleaf pine control
Forest stand height (m)	27.4 (1.9)^{A}	30.2 (2.0)^{B}	24.5 (2.6)^{C}	26.2 (2.9)^{AC}
Forest stand age (year)	75.4 (11.9)^{A}	63.8 (7.9)^{B}	64.6 (12.2)^{B}	57.1 (5.8)^{B}
Canopy closure (%)	73.0 (12.7)^{A}	82.8 (7.9)^{A}	58.6 (17.0)^{B}	75.8 (11.4)^{A}
Pine basal area (m^2/ha)	19.7 (3.9)^{A}	20.6 (5.6)^{A}	18.5 (5.3)^{A}	13.5 (3.5)^{B}
Hardwood basal area (m^2/ha)	0.1 (0.3)^{A}	4.9 (2.4)^{B}	0.1 (0.3)^{A}	3.6 (3.7)^{B}
Hardwood stems 5–14 cm	0.1 (0.3)^{A}	5.1 (3.2)^{B}	0.0 (0.0)^{A}	2.4 (1.4)^{C}
Hardwood stems 15–32 cm	0.1 (0.3)^{A}	0.8 (1.3)^{A,B}	0.1 (0.3)^{A}	2.9 (4.8)^{B}
Foliage density 0–1 m (×100)	14.2 (5.6)^{A}	6.1 (5.2)^{B}	7.8 (2.4)^{B}	6.5 (3.4)^{B}
Foliage density 1–2 m (×100)	5.3 (4.5)^{A}	2.2 (1.9)^{A,B}	1.7 (1.9)^{B}	4.1 (4.5)^{A,B}
Foliage density 2–3 m (×100)	2.6 (2.2)^{A}	1.0 (0.8)^{A,B}	0.8 (0.2)^{B}	2.5 (2.4)^{A}
Grass ground cover (%)	19.8 (22.6)^{A,B}	7.0 (12.7)^{B}	27.5 (22.2)^{A}	8.5 (18.0)^{B}
Dicot fern ground cover (%)	18.0 (10.1)^{A}	48.0 (24.2)^{B}	30.8 (18.8)^{A,B}	72.5 (23.3)^{C}

greater within managed Red-cockaded Woodpecker cluster sites than within control sites in loblolly-shortleaf pine habitat during winter. We did not detect a significant difference in species richness, abundance, or equitability between managed and control sites in longleaf pine during winter (Table 2). We also did not detect a relationship between habitat treatment and avian equitability during either spring or winter.

Management for Red-cockaded Woodpeckers appeared to benefit many bird species during the breeding season. We detected greater abundances of American Kestrels, Northern Bobwhites, Red-cockaded Woodpeckers, Brown-headed Nuthatches (*Sitta pusilla*), Yellow-breasted Chats (*Icteria virens*), Bachman's Sparrows, and Indigo Buntings (*Passerina cyanea*) in sites managed for Red-cockaded Woodpeckers than in control sites in both pine cover types (Table 3). Eastern Wood-Pewees and White-eyed Vireos (*Vireo griseus*) were more abundant in managed woodpecker clusters than in control sites in

TABLE 2. Spring and winter avian community characteristics summarized from bird census point-count sites in Red-cockaded Woodpecker (*Picoides borealis*; RCW) cavity tree clusters and noncluster control sites in loblolly-shortleaf pine and longleaf pine forest types from 1995–1997 on the Angelina National Forest in eastern Texas ($n = 30$ for each treatment; 10 sites × 3 years). Values are means (SD). Within each row, values with the same letter are not significantly different ($P > 0.05$, two-way ANOVA, year × treatment, with Duncan's Multiple Range Test).

Avian community characteristic	Habitat treatment			
	Loblolly-shortleaf pine RCW cluster	Loblolly-shortleaf pine control	Longleaf pine RCW cluster	Longleaf pine control
Spring				
Species richness	10.3 (3.5)^{A}	7.0 (2.8)^{B,C}	7.2 (2.6)^{B}	5.7 (2.7)^{C}
Avian abundance (no.)	31.5 (14.2)^{A}	20.1 (8.8)^{B}	22.0 (11.5)^{B}	13.3 (10.2)^{C}
Equitability (J′)	0.9 (0.1)^{A}	0.8 (0.1)^{A}	0.9 (0.1)^{A}	0.9 (0.2)^{A}
Winter				
Species richness	8.2 (3.6)^{A}	5.4 (2.5)^{B}	6.7 (3.0)^{A,B}	6.8 (3.0)^{A,B}
Avian abundance (no.)	42.3 (27.4)^{A}	27.9 (23.4)^{B}	30.3 (23.6)^{B}	25.8 (25.9)^{B}
Equitability (J′)	0.8 (0.2)^{A}	0.7 (0.2)^{A}	0.8 (0.1)^{A}	0.8 (0.1)^{A}

TABLE 3. Mean number of birds detected per trip during spring summarized from bird census point-count sites in Red-cockaded Woodpecker (*Picoides borealis*; RCW) cavity tree clusters and noncluster control sites in loblolly-shortleaf pine and longleaf pine forest types from 1955–1997 on the Angelina National Forest in eastern Texas (n = 30 for each treatment; 10 sites × 3 years). Values are means (SD). Within each row, values with the same letter are not significantly different ($P > 0.05$; two-way ANOVA, year × treatment, with Duncan's Multiple Range Test).

Species	Habitat treatment			
	Loblolly-shortleaf pine RCW cluster	Loblolly-shortleaf pine control	Longleaf pine RCW cluster	Longleaf pine control
Year round residents				
Wood Duck (*Aix sponsa*)	0.33 (1.0)^{A}	0.07 (0.4)^{A,B}	0.03 (0.2)^{B}	0.0 (0.0)
American Kestrel (*Falco sparverius*)	0.03 (0.2)^{A}	0.0 (0.0)	0.23 (0.8)^{A}	0.0 (0.0)
Northern Bobwhite (*Colinus virginianus*)	0.03 (0.2)^{A}	0.0 (0.0)	0.20 (0.6)^{B}	0.0 (0.0)
Mourning Dove (*Zenaida macroura*)	0.33 (0.9)^{A}	0.10 (0.4)^{A,B}	0.43 (0.8)^{A}	0.03 (0.2)^{B}
Red-bellied Woodpecker (*Melanerpes carolinus*)	0.33 (0.6)^{A}	0.27 (0.6)^{A}	0.33 (0.6)^{A}	0.13 (0.4)^{A}
Hairy Woodpecker (*Picoides villosus*)	0.17 (0.5)^{A}	0.03 (0.2)^{A}	0.03 (0.2)^{A}	0.03 (0.2)^{A}
Red-cockaded Woodpecker (*Picoides borealis*)	2.47 (3.0)^{A}	0.03 (0.2)^{B}	2.37 (2.7)^{A}	0.0 (0.0)
Pileated Woodpecker (*Dryocopus pileatus*)	0.13 (0.3)^{A}	0.10 (0.3)^{A}	0.10 (0.3)^{A}	0.03 (0.2)^{A}
Blue Jay (*Cyanocitta cristata*)	0.47 (0.9)^{A}	0.06 (0.9)^{A,B}	1.07 (1.0)^{B}	1.10 (1.4)^{B}
American Crow (*Corvus brachyrhynchos*)	0.23 (0.7)^{A}	0.53 (1.7)^{A}	0.77 (1.5)^{A}	0.30 (0.7)^{A}
Carolina Chickadee (*Poecile carolinensis*)	0.83 (1.3)^{A}	0.87 (1.2)^{A}	0.13 (0.3)^{B}	0.40 (0.7)^{A,B}
Tufted Titmouse (*Baeolophus bicolor*)	0.37 (0.8)^{A}	0.60 (0.9)^{A}	0.0 (0.0)	0.57 (1.2)^{A}
Brown-headed Nuthatch (*Sitta pusilla*)	2.57 (2.5)^{A}	0.23 (0.6)^{B}	3.0 (3.3)^{A}	0.23 (0.9)^{B}
Carolina Wren (*Thryothorus ludovicianus*)	1.53 (1.6)^{A}	1.60 (1.4)^{A}	0.97 (1.5)^{A}	1.33 (1.4)^{A}
Pine Warbler (*Dendroica pinus*)	8.53 (3.7)^{A}	8.10 (3.7)^{A}	5.20 (3.2)^{B}	3.90 (3.2)^{B}
Northern Cardinal (*Cardinalis cardinalis*)	2.40 (2.3)^{A}	2.17 (1.8)^{A,B}	0.87 (1.9)^{B}	2.37 (4.0)^{A}
Bachman's Sparrow (*Aimophila aestivalis*)	0.83 (1.3)^{A}	0.0 (0.0)	1.63 (1.8)^{B}	0.0 (0.0)
Nearctic-Neotropical migrants and summer residents				
Yellow-billed Cuckoo (*Coccyzus americanus*)	0.10 (0.3)^{A}	0.23 (0.5)^{A}	0.06 (0.3)^{A}	0.13 (0.3)^{A}
Eastern Wood-Pewee (*Contopus virens*)	0.63 (1.1)^{A}	0.10 (0.3)^{B}	0.0 (0.0)	0.07 (0.2)^{B}
Great Crested Flycatcher (*Myiarchus crinitus*)	0.00 (0.0)	0.07 (0.3)^{A}	0.0 (0.0)	0.07 (0.4)^{A}
White-eyed Vireo (*Vireo griseus*)	0.83 (1.3)^{A}	0.0 (0.0)	0.20 (0.7)^{B}	0.17 (0.5)^{B}
Red-eyed Vireo (*Vireo olivaceus*)	0.63 (1.2)^{A}	1.80 (1.7)^{B}	0.0 (0.0)	0.33 (0.5)^{A}
Wood Thrush (*Hylocichla mustelina*)	0.03 (0.2)^{A}	0.17 (0.5)^{A}	0.0 (0.0)	0.07 (0.4)^{A}
Hood Warbler (*Wilsonia citrina*)	0.40 (0.7)^{A}	0.50 (0.9)^{A}	0.13 (0.4)^{A}	0.57 (1.2)^{A}
Yellow-breasted Chat (*Icteria virens*)	2.00 (2.6)^{A}	0.03 (0.2)^{B}	0.87 (1.9)^{C}	0.0 (0.0)
Summer Tanager (*Piranga rubra*)	0.96 (1.2)^{A}	1.23 (1.6)^{A}	0.13 (0.4)^{B}	0.73 (0.9)^{A}
Blue Grosbeak (*Passerina caerulea*)	0.10 (0.4)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Indigo Bunting (*Passerina cyanea*)	3.50 (2.7)^{A}	0.13 (0.3)^{B}	2.87 (2.5)^{A}	0.40 (0.7)^{B}

loblolly-shortleaf pine habitat. Blue Grosbeaks (*Passerina caerulea*) were detected only in managed loblolly-shortleaf pine habitat. A few species had a negative relationship with Red-cockaded Woodpecker management: the Great Crested Flycatcher (*Myiarchus crinitus*), Red-eyed Vireo (*Vireo olivaceus*), Tufted Titmouse (*Baeolophus bicolor*), Wood Thrush (*Hylocichla mustelina*), Summer Tanager (*Piranga rubra*), and Northern Cardinal (*Cardinalis cardinalis*). Abundances of at least eight breeding bird species did not appear to be related to woodpecker management.

During winter in loblolly and shortleaf pine we detected greater abundances of Wood Ducks (*Aix sponsa*), American Kestrels, Red-bellied Woodpeckers (*Melanerpes carolinus*), Red-cockaded Woodpeckers, Pileated Woodpeckers (*Dryocopus pileatus*), Carolina Chickadees (*Poecile carolinensis*), Brown-headed Nuthatches, Golden-crowned Kinglets (*Regulus satrapa*), Pine Warblers (*Dendroica pinus*), and Chipping Sparrows (*Spizella passerina*) within managed sites than within control sites (Table 4). Only Blue Jays (*Cyanocitta cristata*), Yellow-bellied Sapsuckers (*Sphyrapicus varius*; longleaf pine only), and Hermit Thrushes (*Catharus guttatus*) were de-

TABLE 4. Mean number of birds detected per trip during winter summarized from bird census point-count sites in Red-cockaded Woodpecker (*Picoides borealis*; RCW) cavity tree clusters and noncluster control sites in loblolly-shortleaf pine and longleaf pine forest types from 1995–1997 on the Angelina National Forest in eastern Texas (n = 30 for each treatment; 10 sites × 3 years). Values are means (SD). Within each row, values with the same letter are not significantly different ($P > 0.05$; two-way ANOVA, year × treatment, with Duncan's Multiple Range Test).

Species	Habitat treatment			
	Loblolly-shortleaf pine RCW cluster	Loblolly-shortleaf pine control	Longleaf pine RCW cluster	Longleaf pine control
Year round residents				
Wood Duck (*Aix sponsa*)	0.07 (0.4)^{A}	0.0 (0.0)	0.07 (0.04)^{A}	0.0 (0.0)
American Kestrel (*Falco sparverius*)	0.20 (0.5)^{A}	0.0 (0.0)	0.10 (0.3)^{A}	0.0 (0.0)
Mourning Dove (*Zenaida macroura*)	0.0 (0.0)	0.0 (0.0)	0.13 (0.5)^{A}	0.17 (0.7)^{A}
Red-bellied Woodpecker (*Melanerpes carolinus*)	0.60 (1.0)^{A,B}	0.0 (0.0)	0.67 (0.9)^{A}	0.27 (0.5)^{B}
Hairy Woodpecker (*Picoides villosus*)	0.07 (0.3)^{A}	0.0 (0.0)	0.0 (0.0)	0.13 (0.4)^{A}
Red-cockaded Woodpecker (*Picoides borealis*)	2.13 (2.5)^{A}	0.0 (0.0)	1.93 (2.6)^{A}	0.03 (0.2)^{B}
Pileated Woodpecker (*Dryocopus pileatus*)	0.37 (0.7)^{A}	0.10 (0.3)^{B}	0.10 (0.3)^{B}	0.10 (0.3)^{B}
Blue Jay (*Cyanocitta cristata*)	0.06 (0.4)^{A}	0.07 (0.4)^{A}	0.0 (0.0)	0.43 (0.9)^{B}
American Crow (*Corvus brachyrhynchos*)	0.06 (0.3)^{A}	0.20 (0.5)^{A}	0.73 (1.5)^{B}	0.30 (0.9)^{A,B}
Carolina Chickadee (*Poecile carolinensis*)	1.53 (1.8)^{A}	0.73 (1.4)^{B}	0.60 (1.0)^{B}	0.57 (1.1)^{B}
Tufted Titmouse (*Baeolophus bicolor*)	0.73 (1.1)^{A}	0.37 (0.6)^{A,B}	0.23 (0.6)^{B}	0.40 (0.7)^{A,B}
Brown-headed Nuthatch (*Sitta pusilla*)	3.40 (2.6)^{A}	0.33 (0.7)^{B}	3.0 (2.7)^{A}	0.57 (1.1)^{B}
Carolina Wren (*Thryothorus ludovicianus*)	1.10 (1.4)^{A}	1.03 (1.4)^{A}	0.50 (0.8)^{A}	0.90 (1.1)^{A}
Pine Warbler (*Dendroica pinus*)	17.47 (11.3)^{A}	13.00 (8.5)^{B}	8.63 (4.9)^{C}	7.60 (4.9)^{C}
Northern Cardinal (*Cardinalis cardinalis*)	0.63 (0.9)^{A}	0.50 (0.9)^{A}	0.13 (0.4)^{A}	0.53 (1.4)^{A}
Bachman's Sparrow (*Aimophila aestivalis*)	0.0 (0.0)	0.0 (0.0)	0.03 (0.2)	0.0 (0.0)
Temperate zone migrants and winter residents				
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	0.17 (0.4)^{A}	0.13 (0.3)^{A}	0.30 (0.5)^{A}	0.70 (1.0)^{B}
Eastern Phoebe (*Sayornis phoebe*)	0.17 (0.4)^{A}	0.20 (0.5)^{A}	0.07 (0.3)^{A}	0.07 (0.3)^{A}
Golden-crowned Kinglet (*Regulus satrapa*)	0.80 (1.7)^{A}	0.27 (0.7)^{B}	0.03 (0.2)^{B}	0.17 (0.5)^{B}
Ruby-crowned Kinglet (*Regulus calendula*)	1.20 (1.6)^{A,B}	0.70 (1.0)^{B}	0.90 (1.2)^{A,B}	1.47 (1.2)^{A}
Eastern Bluebird (*Sialia sialis*)	0.37 (1.7)^{A}	0.0 (0.0)	0.0 (0.0)	0.07 (0.4)^{A}
Hermit Thrush (*Catharus guttatus*)	0.0 (0.0)	0.10 (0.3)^{A}	0.07 (0.3)^{A}	0.33 (0.7)^{B}
American Robin (*Turdus migratorius*)	0.13 (0.3)^{A}	0.27 (0.7)^{A}	0.40 (1.5)^{A}	0.13 (0.3)^{A}
Yellow-rumped Warbler (*Dendroica coronata*)	1.37 (1.9)^{A}	1.33 (1.8)^{A}	1.13 (1.3)^{A}	2.10 (1.9)^{A}
Chipping Sparrow (*Spizella passerina*)	0.10 (0.3)^{A}	0.0 (0.0)	0.06 (0.3)^{A}	0.0 (0.0)
White-throated Sparrow (*Zonotrichia albicollis*)	0.80 (1.8)^{A}	0.13 (0.7)^{A}	1.43 (4.5)^{A}	0.93 (2.8)^{A}
Dark-eyed Junco (*Junco hyemalis*)	1.60 (3.6)^{A}	0.53 (2.2)^{A}	1.00 (2.6)^{A}	1.10 (2.6)^{A}
American Goldfinch (*Carduelis tristis*)	6.90 (14.2)^{A}	6.33 (17.1)^{A}	7.73 (19.2)^{A}	6.60 (20.0)^{A}

tected less often in managed sites than in control sites during winter. Twelve bird species appeared to have no relationship with woodpecker management during winter.

DISCUSSION

Management for Red-cockaded Woodpeckers, which included hardwood removal from around cavity trees, mulching of midstory and understory vegetation, overstory pine thinning, and prescribed fire, altered forest structure primarily in the midstory, understory, and herbaceous layers. Soil disturbance and reduction of hardwood midstory foliage and thinning of the canopy, which increased light penetration close to the ground, apparently permitted an increase in the density of woody shrubs and grasses. The abundance of species such as Indigo Buntings and Yellow-breasted Chats during the breeding season was associated with increases in shrub layer woody vegetation, as would be expected based on results of previous studies (Conner et al. 1983; Dickson et al. 1984, 1993b; Conner and Dickson 1997). Consistent with Powell et al. (2000), we found no statistical evidence that habitat management for Red-cockaded Woodpeckers was negatively associated with Wood Thrush abundance. The abundance of American Kestrels, Bachman's Sparrows, and Northern Bobwhites, as observed by Wilson et al. (1995), likely are associated with the increase in grasses in the herbaceous layer and the arthropod populations the grasses supported (Collins et al. 2002). The greater abundance of Brown-headed Nuthatches and Red-cockaded Woodpeckers within managed sites likely is associated with these species apparent avoidance of hardwood vegetation (Conner et al. 1983, Conner and Rudolph 1989, Loeb et al. 1992). Brown-headed Nuthatches also are known to respond favorably to thinning of loblolly pine plantations (Wilson and Watts 1999).

The observed increase in breeding bird species richness and abundance in both loblolly-shortleaf and longleaf pine habitats appears to be the community level result of the collective positive relationship of individual species with the increase in shrub layer vegetation and grasses associated with Red-cockaded Woodpecker management. Open forest habitat created by Red-cockaded Woodpecker management in both longleaf and loblolly-shortleaf pine types appears to provide habitat for many mature forest bird species but also permits the presence of some shrub-associated bird species during the breeding season.

Gates and Gysel (1978) suggested that increased openness of forest habitat might increase the rate of nest parasitism by Brown-headed Cowbirds, a distinct possibility in forest habitat in close proximity to agricultural lands. During 3 years of study, we detected Brown-headed Cowbirds only twice in one of the habitat treatments, a managed Red-cockaded Woodpecker cluster in loblolly-shortleaf pine habitat, most likely because agricultural areas were not a significant component of the overall forest landscape.

A positive community level response was detected only in loblolly-shortleaf pine habitat during winter; we did not detect any community level relationships of woodpecker management in longleaf pine habitat during winter. The observed increases in bird species richness and abundance in loblolly-shortleaf pine habitat during winter also may have been associated with favorable bird response to the greater presence of grasses and woody shrub level plants (Conner et al. 1979, Dickson et al. 1995). Although the Henslow's Sparrow is a species of concern known to winter in eastern Texas, we did not detect any individuals during winter surveys in any of the habitat treatments, which probably reflects the difficulty in detecting this species during point counts in winter.

Based on our observations, management for Red-cockaded Woodpeckers appears to have a negative relationship with only a few avian species, none of which are of immediate conservation concern. Some of the species that exhibited declines in abundance were common and ubiquitous species such as Blue Jays and Northern Cardinals. Reductions in the abundances of Great Crested Flycatchers, Red-eyed Vireos, Wood Thrushes, Summer Tanagers, and Northern Cardinals likely were associated with the decrease in hardwood foliage in the overstory and midstory. Red-cockaded Woodpecker management was positively associated with many bird species, including the American Kestrel, Red-cockaded Woodpecker, and Bachman's Sparrow, which are species of serious regional conservation con-

cern. Overall, woodpecker management was associated with an increase in landscape level biodiversity by adding habitat features needed by shrub and grass-associated birds.

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HABITAT USE BY THE BICKNELL'S THRUSH IN THE ESTRIE REGION, QUEBEC

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ABSTRACT.—Concern has been raised that the viability of Bicknell's Thrush (*Catharus bicknelli*) populations is precarious due, in part, to threats to its breeding habitat. Qualitative descriptions of habitat use have suggested that the species breeds primarily in dense, high elevation forests of northeastern North America. However, there is little quantitative information on habitat use patterns, which impedes formulation of effective conservation plans. To address this knowledge gap, we characterized the habitat of 42 sites occupied by Bicknell's Thrushes and 19 unoccupied sites on two mountains in the Estrie region, Quebec. Occupied sites were dominated by balsam fir (*Abies balsamea*) growing at high density, whereas unoccupied sites had a larger component of hardwoods at lower density. We found significant differences in vegetation composition and habitat structure between occupied and unoccupied sites for each mountain separately, and the two combined, though the particular variables distinguishing the two site types varied between the two mountains likely because of differences in management history. Our results show that the structure of occupied habitats may differ among sites even within a single region. However, it was evident that dense balsam fir-dominated habitats were used selectively by Bicknell's Thrushes at both study sites, and that the maintenance of such habitats should be a conservation priority in the Estrie region. *Received 9 October 2001, accepted 6 June 2002.*

Habitat loss and degradation is the most important threat to bird conservation (Bibby 1995). Among the approximately 10,000 extant avian species, 11% currently are susceptible of becoming extinct largely due to habitat destruction or deterioration (Collar and Andrew 1988, Doyle 1997, BirdLife International 2000, International Union for Conservation of Nature and Natural Resources [IUCN] 2000). Consequently, determining the habitat use patterns of species at risk is of crucial importance from a management perspective.

The Bicknell's Thrush (*Catharus bicknelli*) is one of the rarest birds in North America. Its breeding range is restricted to parts of southern Quebec, New Brunswick, and Nova Scotia in Canada, and New York and New England in the United States, and its population size has been estimated at 25,000–50,000 individuals (Rimmer et al. 2001). Due to limited numbers and its sensitivity to habitat degradation, the Bicknell's Thrush recently has been designated a species of special concern in Canada (Committee on the Status of Endangered Wildlife in Canada 1999, Dunn et al. 1999, Nixon 1999), as a top conservation priority in the northeastern United States (Rosenberg and Wells 2000), and as globally vulnerable using IUCN's criteria (BirdLife International 2000, IUCN 2000).

Our understanding of Bicknell's Thrush habitat use is based largely on qualitative information (but see Nixon et al. 2001). Within the United States, the Bicknell's Thrush is considered a strict habitat specialist, occurring almost exclusively in dense, high elevation forests dominated by small, stunted balsam fir (*Abies balsamea*) and red spruce (*Picea rubens*; Wallace 1939, Atwood et al. 1996). In Canada, the species occurs in a wider variety of habitats, including some low elevation coastal and insular evergreen stands with a forest structure (i.e., dense conifers) similar to the higher elevation sites (Erskine 1992, Ouellet 1993). In recent years, the Bicknell's Thrush also has been observed in second growth forests, often with a significant component of hardwoods, following major logging or natural disturbance (Ouellet 1993, Nixon et al. 2001).

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Though the Bicknell's Thrush is of obvious concern to conservation biologists, there have been few quantitative studies of its habitat characteristics (but see Nixon et al. 2001), a necessary first step toward understanding the regulation of distribution and abundance. Our primary objective in this study was to provide a detailed, quantitative description of the vegetation composition and habitat structure of sites occupied and unoccupied by Bicknell's Thrushes on two mountains that represent strongholds for the species in southern Quebec, Mont Mégantic and Mont Gosford.

STUDY AREA AND METHODS

We conducted field work between 3 June and 16 July 1997, and 25 May and 28 July 1998 on Mont Mégantic (45° 27′ N, 71° 09′ W; 1,112 m maximum elevation) and Mont Gosford (45° 18′ N, 70° 52′ W; 1,189 m maximum elevation) which are part of the Appalachian Mountain range, near the Quebec-Maine border. Our study area at Mont Gosford included the Canadian portion of the Gosford massif, not just Mont Gosford itself. Marcotte and Grandtner (1974) provided a detailed description of vegetation types at Mont Mégantic, as did Pellerin (1986) for Mont Gosford. In general, high elevation areas on both mountains are dominated by balsam fir, with increasing abundance of hardwoods, including yellow birch (*Betula alleghaniensis*) and mountain maple (*Acer spicatum*), at lower elevations. Mont Mégantic has not been logged since the late 1950s, and the site now is a provincial conservation park (Marcotte and Grandtner 1974, Gouvernement du Québec 1988), while Mont Gosford was clear cut in some areas during the 1970s and thinned during the 1990s (Comité de Gestion Provisoire de la Forêt Habitée du Mont Gosford 1997).

Site selection.—We studied the elevational range of the Bicknell's Thrush along six routes: four on Mont Mégantic between 600–1,100 m elevation, and two on Mont Gosford between 700–1,090 m. These ranges closely correspond to the entire elevational ranges of both mountains.

We identified occupied and unoccupied sites first during point count censuses along the six routes between 9 June and 23 June 1997, and between 9 June and 2 July 1998. On 80% of census days, skies were clear and winds were weak at most; mist and light rain was intermittent on the other days. Point count stations were located at each 50-m elevation interval, or at most 200 m apart along the route. We surveyed each point count station for 8 min at least three times: twice during morning (04:30–07:30 EST) and once during evening (18:00–21:00), with 2–9 days between consecutive surveys. If we did not observe a Bicknell's Thrush at a station during the first three surveys, we conducted three additional surveys.

To increase our sample size, we identified additional occupied sites for habitat characterization during spot-mapping censuses in five areas of 5–9.5 ha (mean = 7.3 ha), three on Mont Mégantic and two on Mont Gosford. Each area used for spot mapping was located where a Bicknell's Thrush was known to occur, and was censused 8–9 times, including 4–5 visits during morning and 3–4 visits during evening. Eleven of the 22 occupied sites at Mont Mégantic and 9 of the 20 occupied sites at Mont Gosford were located within the spot-mapping census areas, with 1–8 sites per spot-mapping area, and a minimum distance of 100 m between sites.

We considered a site occupied if we observed a Bicknell's Thrush on at least one occasion. Unoccupied sites were located either within the elevational range of the species where no Bicknell's Thrushes had been observed, or ≤100 m elevation below the lower limit of the elevational range. It was necessary to include sites below the lower limit of the elevational range in order to achieve sufficient sample size of unoccupied sites, but the distance was minimized to ensure that all sites were at relatively high elevation. We characterized a total of 22 occupied and 12 unoccupied sites at Mont Mégantic, and 20 occupied and seven unoccupied sites at Mont Gosford. The exact coordinates of all sites can be found in Connolly (2000).

Habitat characterization—At each site, we characterized the habitat along a 50-m transect oriented at approximately 45° to the upslope-downslope axis. In occupied sites, the midpoint of each transect was located where a bird had been observed. In unoccupied sites, the midpoint corresponded to the position of the observer during the censuses. We recorded elevation for the midpoint of each transect using a Thommen altimeter (Thommen, Waldenburg, Switzerland).

We established 10 5-m × 1-m plots on alternating sides of each 50-m transect line, and chose five plots at random for detailed habitat characterization. In each plot we characterized eight vegetation composition variables and 22 habitat structure variables. For vegetation composition, the importance value of seven tree species and the shrub layer were calculated as the mean of the percentage of total basal area and the percentage of total number of stems accounted for by a given taxon within a 5-m × 1-m plot. We measured habitat structure variables to characterize the densities and cover of living trees, dead trees and fallen branches, tree stumps, herbaceous plants, mosses, ferns, lichens, bare rock, and leaf litter. We counted dead fallen branches across the entire 50-m transect. Detailed descriptions of each variable and how it was measured are provided in the Appendix.

Statistical analyses—As a single estimate for each variable on a given transect, we used the mean value across the five plots. Our analyses aimed to fulfill two goals, (1) to provide a visual summary of how habitat structure and vegetation varied among occupied and unoccupied sites on the two mountains, and (2) to test whether the differences were statistically significant.

The first goal was achieved using ordination techniques. Detrended correspondence analysis (DCA) was designed specifically for vegetation data (Jongman et

al. 1995), and we used it for our vegetation analysis. DCA assumes unimodal distributions of plant species along gradients, and thus avoids the "horseshoe effect," which is an artifactual curvilinear relationship between ordination axes that often arises when other ordination techniques, such as principle components analysis (PCA), are used for vegetation data (Jongman et al. 1995). PCA is an ordination method ideal for variables that are expected to vary linearly along gradients (Jongman et al. 1995), and thus we used PCA to analyze the habitat structure data.

We performed the DCA of tree and shrub importance values (see Appendix) using Canoco ver. 4.0 (ter Braak and Smilauer 1998). Importance values were ln + 1 transformed prior to analysis. We performed the PCA of the 22 habitat structure variables using SAS ver. 7.0 (SAS Institute, Inc. 1998). The variables CANOP, SCANOP, USHRUB, HERB, TOTC, DENS5, and DENS10 (see Appendix) were not transformed, LITTER was arcsin-square root transformed, and other variables were ln + 1 transformed.

To test for differences between occupied and unoccupied sites (our second goal), we used discriminant function analyses (DFA). For the first two axes from each of the DCA and PCA (these represent the major axes of variation in vegetation and habitat structure, respectively), we performed DFAs for each mountain separately, and for the entire data set using SYSTAT ver. 6.0 (SPSS, Inc. 1996). The large number of variables relative to the number of samples precluded using the full set of variables in a DFA (Stevens 1996). The percentage of sites classified correctly by the discriminant functions was determined using both the entire data set, as well as with a jackknife technique in which sites were classified with functions calculated using all of the data except the site being classified (SPSS, Inc. 1996). Variables that contributed most to distinguishing between occupied and unoccupied sites were identified as those that were highly correlated with the discriminant functions (Stevens 1996).

RESULTS

We found Bicknell's Thrushes between 925 m and 1,100 m on Mont Mégantic, and between 775 m and 1,090 m on Mont Gosford. On Mont Mégantic, the percentage of sites occupied dropped markedly below about 925 m (96% above 950 m, 12% at 900–950 m, and 0% below 900 m). The pattern was more gradual on Mont Gosford (75% above 950 m, 67% at 900–950 m, and 56% below 900 m).

Significant differences between occupied and unoccupied sites were evident in the DCA of vegetation composition variables (Fig. 1), in the PCA of habitat structure variables (Fig. 2), and in the DFA (Table 1). In the DFA, the classification functions correctly identified ≥90% of occupied sites and ≥79% of unoccupied sites using the raw data set (Table 1); the jackknife technique produced identical results.

Axis 1 of the DCA (Fig. 1) explained 39% of the variance in vegetation composition, and corresponded to a gradient from dominance by balsam fir at low values (occupied sites) to increasing importance of hardwoods at high values (unoccupied sites). While it appears that the importance of white birch (*Betula papyrifera*) was associated with occupied sites (Fig. 1), this result was due largely to only six sites (10% of all sites) which had either very large or small importance values, rather than to a consistent difference among occupied and unoccupied sites (see Connolly 2000). On Mont Mégantic, the difference in vegetation composition between occupied and unoccupied sites was greater than on Mont Gosford, as revealed both by visual inspection of the ordination diagram (Fig. 1) and by the stronger correlation of DCA1 with the discriminant function for Mont Mégantic (−0.93) relative to Mont Gosford (−0.67; Table 1). Axis 2 explained only 15% of the variance in vegetation composition, and did not appear to distinguish between occupied and unoccupied sites, or between mountains.

Patterns of variation in habitat structure among sites were relatively complex. PCA1, explaining 31% of the variation, corresponded largely to a gradient of tree density (DENS5, DENS10, TOTA, TOTB, TOTC), with low values on PCA1 indicative of sites with low density, tall canopy, and relatively abundant herbs and lichen (and vice versa, see Fig. 2). PCA2, explaining 20% of the variation, reflected a gradient from sites with relatively short shrub canopies, abundant snags (large standing dead trees) and moss, and relatively high tree density at high values, to the opposite conditions at low values. Both visual inspection of the ordination (Fig. 2), and the correlations of the PCA axes with the discriminant function (Table 1) showed that occupied and unoccupied sites were distinguished primarily along PCA1 on Mont Gosford, but primarily along PCA2 on Mont Mégantic (occupied sites at high values). As for Mont Mégantic, occupied sites at Mont Gosford tended toward higher values on PCA2 than unoccupied sites, though the difference was relatively slight.

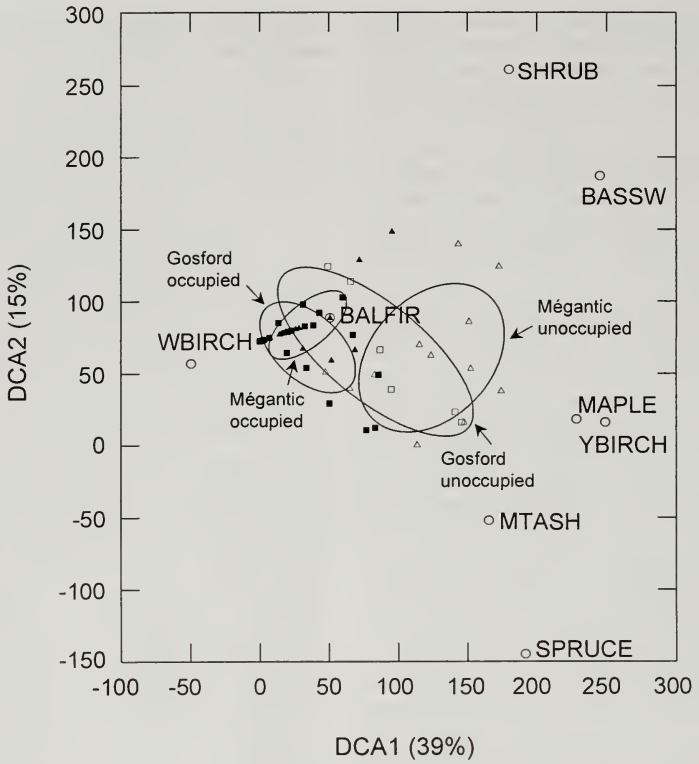

FIG. 1. Detrended correspondence analysis (DCA) showing variation in vegetation composition among sites either occupied (n = 42) or unoccupied (n = 19) by Bicknell's Thrushes on Mont Mégantic and Mont Gosford, southern Quebec, Canada. Axes 1 and 2 accounted for 39% and 15%, respectively, of the variation among sites. Ellipses represent Gaussian bivariate ellipses (± 0.7 SD) for each site type. Solid and empty triangles represent occupied and unoccupied sites, respectively, on Mont Mégantic. Solid and empty squares represent occupied and unoccupied sites, respectively, on Mont Gosford. Circles represent tree and shrub species.

DISCUSSION

Our study has provided one of the most detailed quantitative characterizations to date of the vegetation composition and habitat structure at sites both occupied and unoccupied by Bicknell's Thrushes in the same study area (see also Nixon et al. 2001).

Vegetation composition.—Bicknell's Thrushes selectively occupied high elevation coniferous stands; on Mont Mégantic and Mont Gosford we found Bicknell's Thrushes above 925 m and 775 m elevation, respectively, in forests dominated by balsam fir. Bicknell's Thrushes did not occupy stands with abundant hardwoods. In fact, mountain maple, yellow birch, and American basswood (*Tilia americana*) were entirely absent from occupied sites on the two mountains surveyed. Thus, the presence of these tree species may serve as a crude indicator for the absence of Bicknell's Thrushes in forests of southern Quebec.

Recent surveys conducted in two other regions of Quebec, Charlevoix and Gaspésie, also indicate that Bicknell's Thrushes are unlikely to use mixed forest sites (Y. Aubry and GS unpubl. data). These results contrast markedly with Ouellet (1993), who reported observing more Bicknell's Thrushes in mixed than coniferous forests in Quebec. However, Ouellet (1993) did not provide quantitative criteria for distinguishing "coniferous" and "mixed" forests. In New Brunswick, Bicknell's Thrushes also were found in stands with a significant hardwood component, though at relative low densities (Nixon et al. 2001; D. Busby pers. comm.). Because pure coniferous stands in New Brunswick have been largely eliminated through logging, Bicknell's

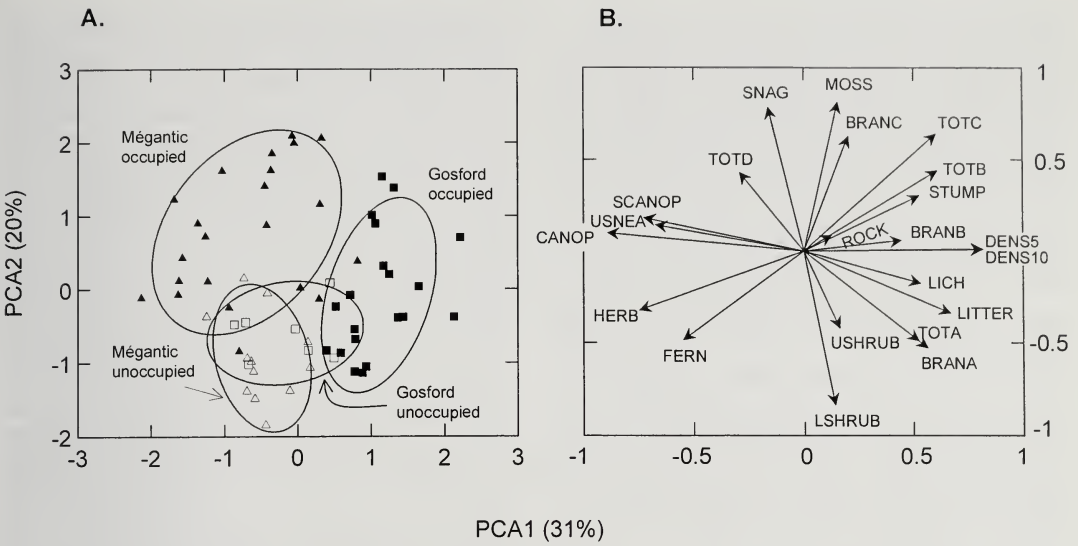

FIG. 2. Principal components analysis (PCA) showing variation in habitat structure among sites either occupied (n = 42) or unoccupied (n = 19) by Bicknell's Thrushes on Mont Mégantic and Mont Gosford, southern Quebec, Canada. Axes 1 and 2 accounted for 31% and 20%, respectively, of the variation among sites. Ellipses represent Gaussian bivariate ellipses (± 1 SD) for each site type. Solid and empty triangles represent occupied and unoccupied sites, respectively, on Mont Mégantic. Solid and empty squares represent occupied and unoccupied sites, respectively, on Mont Gosford. (A) Site distribution. (B) Factor pattern. The coordinate of the tip of a given arrow on a given axis is the Pearson correlation coefficient of the variable with that axis.

Thrushes might thus be constrained to use alternative habitat types. Together, these studies suggest that the Bicknell's Thrush uses dense conifer-dominated habitats when available, but may use alternative habitats as well.

Habitat structure.—There were significant

TABLE 1. Results of discriminant function analyses (DFA) revealing significant differences between sites occupied and unoccupied by Bicknell's Thrushes on Mont Mégantic and Mont Gosford, southern Quebec, Canada, 1997–1998. Correlations are shown between each variable, ordination axes from a vegetation data analysis (DCA) and a habitat structure analysis (PCA), and the canonical function produced by the DFA.

	Geographic comparison		
Variable	All sites	Mégantic sites	Gosford sites
DCA1	−0.95	−0.93	−0.67
DCA2	0.29	0.42	0.06
PCA1	0.33	−0.16	0.94
PCA2	0.72	0.83	0.38
Wilk's lambda	0.42	0.22	0.36
Approximate F	19.05	26.38	9.57
P	<0.0001	<0.0001	0.0001
Eigenvalue	1.36	3.64	1.74
Group centroids			
Occupied sites	0.77	1.37	0.75
Unoccupied sites	−1.71	−2.51	−2.15
Correct classification - raw dataset (%; identical to jackknife results)			
Occupied sites	90	100	90
Unoccupied sites	79	92	86

differences in habitat structure between occupied and unoccupied sites in the Estrie region. Some of the measured variables that distinguished occupied from unoccupied sites may be directly related to habitat selection; others may be only correlated with the relevant habitat characteristics. Our data do not permit resolution of these alternatives, but they do allow interpretation of the potential relevance of different habitat characteristics in light of what is known about the species. The interpretations that follow focus on selected variables of potentially direct relevance to Bicknell's Thrush biology, and may be considered hypotheses that await further testing.

We have confirmed the use of habitat with very high tree density by the Bicknell's Thrush. Nest predation has been shown to be severe in certain areas and years (Wallace 1939, Rimmer et al. 2001), and the use of dense habitat might be beneficial in making visual detection by predators more difficult (Martin 1992). Sites occupied by Bicknell's Thrushes on Mont Mégantic also were characterized by a greater abundance of snags than unoccupied sites. Wallace (1939) noted large numbers of dead trees in habitat occupied by the species, and this may have been related to the severe climatic conditions prevailing at high elevations. Miller-Weeks and Smoronk (1993) found that most areas of high elevation spruce-fir habitat in New England and the Adirondack region of New York showed high levels of tree mortality during the 1980s. However, abundant snags may attract male Bicknell's Thrushes as they have been observed using snags as song perches (VC and GR pers. obs.).

Occupied sites on Mont Mégantic were characterized by greater percent ground cover of moss than unoccupied sites. This is typical of the wet and cool climate of high elevations (Reiners and Lang 1979, Sabo and Holmes 1983), and the correlation with Bicknell's Thrush habitat use may be related to nest construction. Wallace (1939) noted that the use of fresh moss was an outstanding structural feature of Bicknell's Thrush nests and that no other birds in that region (Mt. Mansfield) built nests with as much moss (see also Rimmer et al. 2001).

Differences between mountains.—We found striking differences in habitat structure, and to a lesser degree vegetation composition, between occupied sites on the two mountains (Figs. 1 and 2). Contrasting histories of forest harvesting and management may be responsible for these differences. Because of more recent logging, forests on Mont Gosford are younger than those on Mont Mégantic, and therefore had a lower canopy, higher density, fewer snags, and less *Usnea*, a slow growing lichen (Fig. 2). Younger forests also typically are more diverse, consistent with our observation of a greater presence of spruce and white birch on Mont Gosford (Fig. 1). Recent logging may well be responsible for the greater similarity of occupied and unoccupied sites in vegetation composition at Mont Gosford than at Mont Mégantic. The differences we observed between mountains imply that the Bicknell's Thrush uses a range of vegetation composition and habitat structure conditions within dense balsam fir dominated forests.

Management and conservation implications.—The Bicknell's Thrush is a species of great conservation concern both locally and globally. Its future depends upon the conservation of both its breeding and wintering habitat. Our results provide new information relevant in this context.

We found that habitat used on different mountains, separated by only 30 km, can differ in vegetation composition and habitat structure. Thus, caution must be taken when assessing habitat suitability of a site on the basis of information obtained from another site or another region.

While our results show that the Bicknell's Thrush occupies mature as well as relatively young (25–40 year-old) second growth stands, it seems to prefer a specific vegetation composition within these forests, specifically a dominance of balsam fir and low density of several deciduous species. Silvicultural practices that would alter such vegetation composition are likely to be detrimental to the species. For example, recolonization of a logged site by balsam fir can be delayed considerably by the aggressive growth of species such as mountain maple (Archambault et al. 1998), thereby extending the period of time in which the habitat is unsuitable for Bicknell's Thrushes.

Though the Bicknell's Thrush shows some flexibility with respect to the structure of oc-

cupied habitat, it is consistently associated with high tree density. Precommercial thinning is a common silvicultural practice in coniferous forests, and consists of reducing stem density in young second growth stands in order to favor growth of the largest individuals of target species. Thinning likely has a negative impact on the Bicknell's Thrush by reducing the extent of very dense habitat. Alternatives to large scale thinning operations need to be developed to insure the maintenance of sufficient amounts of habitat suitable for Bicknell's Thrushes. The establishment of a mosaic of thinned and unthinned patches, or the maintenance of large islands of unthinned habitat, are two such alternatives whose merit should be assessed.

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APPENDIX. Description of vegetation composition and habitat structure variables recorded at sites occupied (n = 42) and unoccupied (n = 19) by Bicknell's Thrushes on Mont Mégantic and Mont Gosford, southern Quebec, Canada, 1997–1998.

Variable	Description
BALFIR	Importance value of balsam fir (*Abies balsamea*). Importance values were calculated as the mean of the percentage of total basal area and the percentage of total number of stems accounted for by a given taxon within a 5-m × 1-m plot.
SPRUCE	Importance value of red and white spruces (*Picea rubens* and *P. glauca*).
WBIRCH	Importance value of white birch (*Betula papyrifera*).
YBIRCH	Importance value of yellow birch (*Betula alleghaniensis*).
MTASH	Importance value of mountain ash (*Sorbus americana*).
MAPLE	Importance value of mountain maple (*Acer spicatum*).
SHRUB	Importance value of shrub species: smooth serviceberry (*Amelanchier laevis*), red-berried elder (*Sambucus racemosa*), spiny swamp currant (*Ribes lacustre*), skunk current (*Ribes glandulosum*), swamp red current (*Ribes triste*), and red raspberry (*Rubus idaeus*).
DENS5, DENS10	Vegetation density indices recorded using a 1-m × 1-m checkerboard with 20-cm × 20-cm squares held at breast height at a distance of 5 m and then 10 m from the midpoint of the 50-m transect where an observer recorded the number of partial and complete dark squares that could be seen (maximum = 13 complete squares). These measures were taken in two to four directions at 90° from one another. Vegetation density indices were calculated separately for the data at 5 m (DENS5) and 10 m (DENS10) using the following equation: $\text{DENS} = [\Sigma(26 - (2c_d + p_d))]/n$, where c_d is the number of complete squares in direction d, p_d is the number of partial squares in direction d, and n is the number of directions. A value of 26 indicates a very high density; a value of 0 indicates low density.
TOTA, TOTB, TOTC, TOTD	The number of tree stems (all species) with diameter <2.5 cm (TOTA), 2.5–5.0 cm (TOTB), 5.1–10.0 cm (TOTC), and >10.0 cm (TOTD) recorded within each 5-m × 1-m plot. Diameter was measured 20 cm above ground.
BRANA, BRANB, BRANC	The number of dead fallen trees or branches on the ground with diameter 2.5–5.0 cm (BRANA), 5.1–10.0 cm (BRANB), and >10.0 cm (BRANC), counted across the 50-m transect.
SNAG	The number of snags (standing dead trees >2 m high) recorded within each 5-m × 1-m plot.
STUMP	The number of tree stumps (<1 m high) recorded within each 5-m × 1-m plot. Stumps created both by natural means and by cutting are included in this number.
MOSS, HERB, FERN, LICH, ROCK, LITTER	Percent ground cover of MOSSes, HERBaceous plants, FERNs, LICHens, bare ROCK, and leaf LITTER estimated visually within each 5-m × 1-m plot.
USNEA	The relative abundance of *Usnea* spp. (a slow-growing lichen) within each 5-m × 1-m plot (1 = absent, 2 = present in low abundance, 3 = present in moderate abundance, 4 = present in high abundance).
CANOP, SCANOP, USHRUB, LSHRUB	The mean height in meters of the canopy (CANOP), subcanopy (SCANOP), and upper and lower shrub (USHRUB and LSHRUB) layers estimated visually within each 5-m × 1-m plot.

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FORAGING BEHAVIOR AND MICROHABITAT USE OF BIRDS INHABITING COASTAL WOODLANDS IN EASTCENTRAL ARGENTINA

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ABSTRACT.—We examined foraging behavior and microhabitat use of four passerine bird species inhabiting an old growth coastal woodland in Buenos Aires Province, Argentina. Based on foraging maneuvers, we identified two groups: (1) nonaerial foragers formed by Tropical Parulas (*Parula pitiayumi*) and Masked Gnatcatchers (*Polioptila dumicola*) that hopped on branches and twigs while searching and gleaning prey from the nearby foliage, and (2) aerial foragers formed by White-crested Tyrannulets (*Serpophaga subcristata*) and Small-billed Elaenias (*Elaenia parvirostris*) that searched for and detected prey while perched, and captured it from foliage or in the air. Nonaerial foragers found prey primarily in the canopy while aerial foragers captured prey at all heights in the woodland. Tree species selection was similar among the four species. All bird species disproportionately foraged in *Scutia buxifolia* and avoided the use of *Ligustrum lucidum* trees. Our results indicate that these bird species differed in microhabitat selection in old growth coastal woodland, and that nonaerial foragers were more sensitive to foliage architecture and foliage height distribution than aerial foragers. These results illustrate the importance of woodland logging to bird densities, and provide basic information for effective management. *Received 19 September 2001, accepted 5 June 2002.*

RESUMEN.—Nosotros estudiamos el comportamiento de alimentación y el uso de microhábitats de cuatro especies passeriformes que habitan bosques costeros maduros de la Provincia de Buenos Aires, Argentina. Considerando las maniobras de alimentación encontramos dos grupos: (1) las recolectoras, formado por Pitiayumí (*Parula pitiayumi*) y Tacuarita Azul (*Polioptila dumicola*), las cuales saltando por las ramas y ramitas buscan y recolectan presas desde el follaje cercano, y (2) las cazadoras por revoloteo, formado por Piojito Común (*Serpophaga subcristata*) y Fiofío Pico Corto (*Elaenia parvirostris*), que buscan y detectan presas desde una percha y, usando tácticas aéreas, capturan las presas desde el follaje o en el aire. Las especies recolectoras capturan sus presas principalmente en el dosel del bosque, mientras que las cazadoras por revoloteo se alimentan en todas las alturas. El uso de las especies arbóreas del bosque fue similar para las cuatro especies de aves. Todas seleccionaron alimentarse en árboles de *Scutia buxifolia* y evitaron usar los de *Ligustrum lucidum*. En general, las especies de aves difieren en su selección de los microhábitats en el bosque costero maduro; las especies recolectoras fueron más afectadas por la arquitectura del follaje y la abundancia de cobertura en altura que las especies cazadoras por revoloteo. Los resultados obtenidos ayudan a comprender los efectos del talado del bosque sobre la densidad de aves, y proveen información básica para su efectivo manejo.

Studies of foraging behavior show how birds use their habitat and allow identification of environmental features that could be influencing bird populations. Vegetation structure provides opportunities and constraints that determine how and where birds detect and capture their prey (Holmes 1990). Leaf morphology, arrangement of leaves on branches, foliage height distribution, and other aspects of foliage architecture have a strong influence on bird foraging behavior (Sabo 1980, Franzreb 1983, Robinson and Holmes 1984, Holmes and Recher 1986, Robinson 1992). These patterns, mostly identified through detailed field studies, also have been supported by experimental aviary studies (Emlen and DeJong 1981; Whelan 1989, 2001; Parrish 1995). As a consequence of these influences, bird species selectively forage in certain tree species, plant life forms, and at particular heights (Holmes and Robinson 1981, Airola and Barrett 1985, Morrison et al. 1986, Adams and Morrison 1993, Sodhi and Paszkowski 1995, Gabbe et al. 2002). These choices ultimately can determine which species survive in a particular habitat.

Little is known about bird foraging ecology in old growth forest and woodlands of southern South America. Such information is important because human activities could be promoting bird population declines in some areas

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(Willson et al. 1994, Aleixo 1999, Cueto and Lopez de Casenave 2000a). Thus, basic understanding of the ecological requirements of bird species inhabiting forest habitats, critical for effective management decisions, is lacking. In this paper, we examine foraging behavior and microhabitat use of White-crested Tyrannulets (*Serpophaga subcristata*), Small-billed Elaenias (*Elaenia parvirostris*), Masked Gnatcatchers (*Polioptila dumicola*), and Tropical Parulas (*Parula pitiayumi*), four species common in coastal woodlands of eastcentral Argentina (Cueto and Lopez de Casenave 2000b). We analyzed frequency of use of different tree species and foliage height where birds captured their prey, and compared this use with relative abundance of tree species and vertical distribution of foliage in an old growth coastal woodland of eastcentral Argentina. We addressed the following questions. (1) Do bird species use the same foraging maneuvers to detect and attack prey? (2) Are there differences in foraging substrate among bird species? (3) Do bird species use the same tree species to search and capture prey? (4) Are there differences in foraging height among bird species?

METHODS

Study area.—We conducted this research in old growth woodland of the Private Reserve El Destino (35° 08′ S, 57° 25′ W; 2,400 ha) on the shore of de la Plata River, Buenos Aires Province, Argentina. This reserve is part of the Biosphere Reserve Parque Costero del Sur. Dominant tree species in El Destino are *Scutia buxifolia* (Rhamnaceae) and *Celtis tala* (Ulmaceae); other less abundant tree species include *Ligustrum lucidum* (Oleaceae), *Schinus longifolius* (Anacardiaceae), *Jodina rhombifolia* (Santalaceae), and *Sambucus australis* (Caprifoliaceae; Cueto and Lopez de Casenave 2000a). A detailed description of the vegetation of El Destino is presented in Cagnoni et al. (1996). The climate is wet, warm temperate, with hot summers and mild winters. Frosts are infrequent because of the proximity to the river. Mean annual precipitation is 88.5 cm (n = 10 years); the rainiest months are January and February (summer). Mean maximum temperature (January) is 27.5° C and the mean minimum temperature (July) is 5.9° C.

Vegetation measurements.—We quantified vegetation structure and composition during December 1992 and March 1993. Eight plots (30 × 30 m) were randomly located in the old growth woodland. In the center of each plot, we established a 15-m transect in each of the four cardinal directions. We sampled vegetation at 30 random points along each transect by erecting a rod marked at 1-m intervals at each point and recording the height and species identity of vegetation contacting the rod. The horizontal cover of each tree species was calculated as the percentage of points at which the species was present. We estimated a mean value over the four transects for each plot. We depicted a profile of foliage cover as the percentage of points with contacts at 1-m intervals.

Bird foraging behavior.—We recorded the foraging behavior of White-crested Tyrannulets, Small-billed Elaenias, Masked Gnatcatchers, and Tropical Parulas during the breeding season (October to March) during 1994–1995 and 1995–1996, and on occasional visits during autumn and winter, 1995. During each sampling period, we systematically walked through the study area and observed as many different birds as possible. When a foraging bird was sighted, we recorded foraging maneuver, substrate from which food was taken or toward which the attack was directed, height above ground (to the nearest m), plant species, and (when possible) prey taken. We defined the following foraging maneuvers: (1) glean, when a perched or walking bird took prey items from the surface of a nearby substrate; (2), probe, when a bird's beak penetrated the substrate in pursuit of subsurface prey items; (3) hover, when a flying bird took prey items from the surface of a substrate; and (4) sally, when a flying bird pursued aerial prey items. Substrates considered were foliage, twigs, branches, and air. We recorded only the first attack for each individual encountered, because sequential observations of repeated foraging maneuvers by the same individual are not independent (Hejl et al. 1990, Recher and Gebski 1990).

Statistical analysis.—We evaluated tree species use with the Chi-square goodness-of-fit test. We estimated expected frequencies of tree use from the relative cover of each tree species. We tested the hypothesis that observed distribution of foraging maneuvers among tree species for each bird species was the same as the expected distribution generated from relative cover of tree species.

We also evaluated foraging height use with the Chi-square goodness-of-fit test. We segregated foraging height data into 1-m height categories. We estimated expected frequencies of height use from the profile of foliage cover. The lowest category (0–1 m above the ground) was not included in these estimates because the birds we observed did not forage at this height. We tested the hypothesis that observed distribution of foraging heights for each bird species was the same as the expected distribution of foraging height generated from the profile of foliage cover.

Chi-square goodness-of-fit tests should not be used if >20% of the cells of expected frequencies are <5, or when any expected frequency is <1 (Siegel and Castellan 1988). To avoid that problem, we combined adjacent categories in some cases to raise the expected values. A consequence of that procedure was the reduction of degrees of freedom. Statistical significance was set at $P \leq 0.05$.

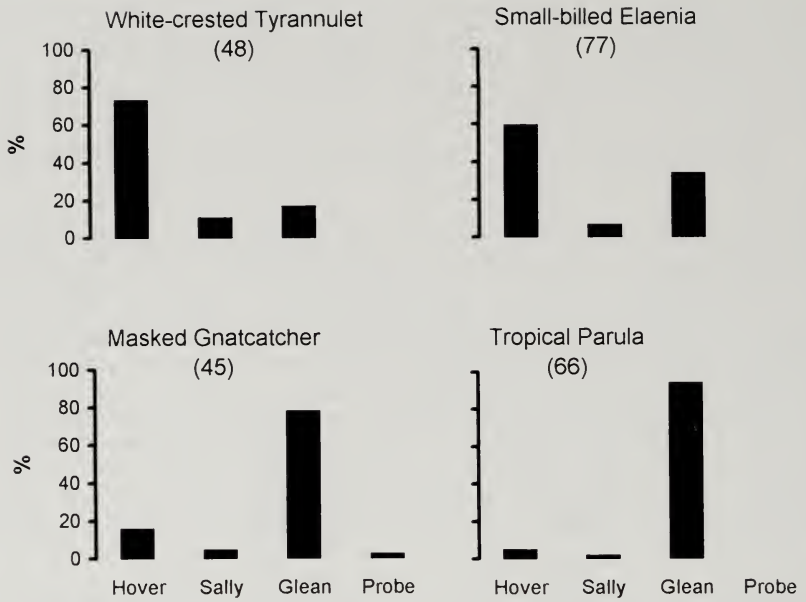

FIG. 1. White-crested Tyrannulets and Small-billed Elaenias most frequently hovered to capture prey, while Masked Gnatcatchers and Tropical Parulas captured prey mostly by gleaning. Data are from old growth coastal woodlands of El Destino Reserve, Buenos Aires, Argentina, 1994–1996. Numbers of individual birds are in parentheses.

RESULTS

Bird attacks were directed mainly at nonflying prey (i.e., glean and hover; Fig. 1). Tropical Parulas and Masked Gnatcatchers used glean as their principal maneuvers, although the first was more stereotyped (>90% of attacks were performed using glean maneuvers). The Masked Gnatcatcher was the only species to probe for prey. White-crested Tyrannulets and Small-billed Elaenias most frequently hovered to capture prey.

The four species concentrated their foraging mainly on foliage (Fig. 2). Twigs also were used, but in low frequencies. White-crested Tyrannulets and Small-billed Elaenias frequently captured prey in the air, and Masked Gnatcatchers used branches more than the other three species.

Foraging height distribution differed significantly among bird species (Fig. 3). Tropical Parulas and Masked Gnatcatchers captured prey predominantly in the canopy of the woodland ($\chi^2_6 = 38.4$, $P < 0.0001$, and $\chi^2_4 = 15.9$, $P = 0.003$, respectively). In contrast, White-crested Tyrannulet and Small-billed Elaenia foraging heights were similar to the available foliage height distribution ($\chi^2_4 = 3.0$, $P = 0.56$, and $\chi^2_6 = 10.4$, $P = 0.11$, respectively).

Tree species were not used by birds in proportion to their availability (Table 1). *Scutia buxifolia* was used to a much greater degree than its relative abundance, and *Ligustrum lucidum* was avoided by the four species. *Celtis tala* frequently was used by Tropical Parulas and White-crested Tyrannulets and in proportion to its availability by Small-billed Elaenias and Masked Gnatcatchers. The other tree species had low cover and rarely were used by the four bird species.

DISCUSSION

The birds we studied in the old growth woodland of El Destino located and captured prey mainly in the tree foliage, using two maneuvers. Tropical Parulas and Masked Gnatcatchers hopped along the branches and twigs capturing prey by gleaning them from nearby foliage. White-crested Tyrannulets and Small-billed Elaenias searched and detected prey while perched, and captured them from foliage using aerial maneuvers. These prey attack maneuvers are common behaviors of foliage-dwelling birds in a variety of woodland

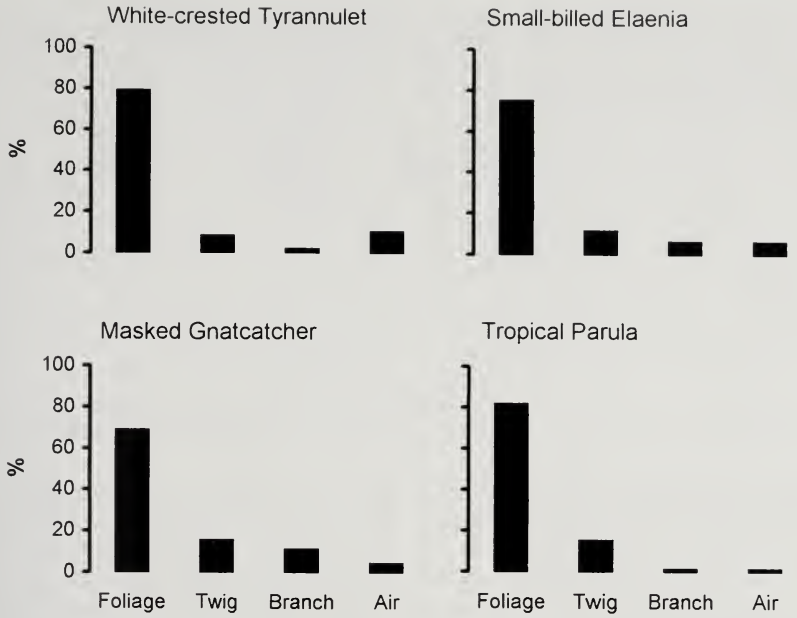

FIG. 2. The four passerine species concentrated their foraging mainly on the foliage substrate in old growth coastal woodlands of El Destino Reserve, Buenos Aires, Argentina, 1994–1996. Sample sizes are the same as in Fig. 1.

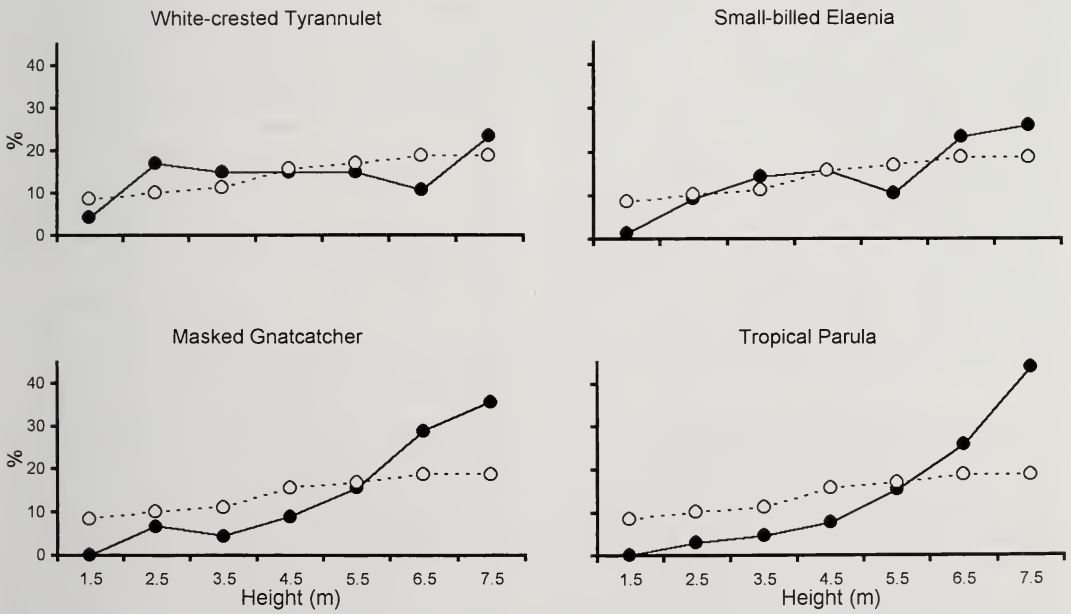

FIG. 3. The distribution of foraging heights (solid circles) of White-crested Tyrannulets and Small-billed Elaenias were similar to the height distribution of available foliage (open circles), while Masked Gnatcatchers and Tropical Parulas captured prey predominantly in the canopy. Data are from old growth coastal woodlands of El Destino Reserve, Buenos Aires, Argentina, 1994–1996. Sample sizes are the same as in Fig. 1.

TABLE 1. Tree species use (%) by four passerine species were not in proportion to tree cover availability (%) in old growth coastal woodlands of El Destino Reserve, Buenos Aires, Argentina, 1994–1996. *Scutia buxifolia* was used disproportionately, and *Ligustrum lucidum* was avoided by the four passerine species. For this analysis we excluded attacks on flying prey.

Tree species	Cover	White-crested Tyrannulet	Small-billed Elaenia	Masked Gnatcatcher	Tropical Parula
Scutia buxifolia	49.3	62.5	63.8	76.7	58.5
Celtis tala	27.6	32.5	27.5	23.3	40.0
Ligustrum lucidum	17.2	—	1.5	—	1.5
Jodina rhombifolia	3.7	5.0	2.9	—	—
Sambucus australis	1.4	—	4.3	—	—
Schinus longifolius	0.8	—	—	—	—
n		40	69	43	65
χ^2_3		8.8	13.1	16.8	17.8
P		0.032	0.004	0.0008	0.0005

and forest habitats (Eckhardt 1979, Holmes et al. 1979, Fitzpatrick 1980, Airola and Barrett 1985, Recher et al. 1985, Carrascal et al. 1987, Sodhi and Paszkowski 1995). The convergence on a small number of ways that birds capture prey suggests that forest structure constrains how birds encounter and attack prey and, in combination with food abundance, provides a set of foraging opportunities that determines which bird species inhabit a given forest habitat. Thus, forest structure could influence the composition of bird assemblages (Holmes and Robinson 1981, Whelan 2001).

Robinson and Holmes (1982, 1984) suggested that prey detectability for gleaning birds is strongly affected by leaf morphology and arrangement (e.g., size, shape, petiole length, and distribution along branches), while birds capturing prey by hovering are less affected by foliage architecture. Experimental aviary studies support this conclusion (Whelan 2001). Thus, we expected that nonaerial foragers in El Destino woodland would be more restricted in use of tree species and heights for foraging than would aerial foragers.

With respect to foraging heights, our results were consistent with those expectations. Tropical Parulas and Masked Gnatcatchers selectively attacked their prey in the canopy of the woodland, while White-crested Tyrannulets and Small-billed Elaenias foraged at all heights. Woodland canopy was dominated by *Scutia buxifolia* and *Celtis tala* (Cueto and Lopez de Casenave 2000a), which have dense foliage of small leaves on short petioles. These features of the foliage could facilitate access to birds that capture prey by gleaning in the nearby substrate (Whelan 1989, 2001). In contrast, the subcanopy had more sparse foliage and aerial foragers used these areas because their search or capture maneuvers were facilitated.

The selection of tree species was partly consistent with our expectations, because all bird species selected *Scutia buxifolia* for capturing prey and avoided *Ligustrum lucidum*. The avoidance of *Ligustrum lucidum* by nonaerial foragers could be related to the morphology and arrangement of leaves of this tree. *Ligustrum lucidum* foliage has large (7–13 cm) leaves with long (1–2 cm) petioles distributed in isolated form along the branches. In addition, *Ligustrum lucidum* also has coriaceous leaves which is an antiherbivore defense (Crawley 1983), so their foliage may support a lower arthropod abundance. This also could contribute to their avoidance by the aerial foragers as well.

Holmes (1990) concluded that patterns of resource use by bird species inhabiting forest habitats were influenced by the plant species present (which influence the type of food resource available) and their life forms (which affect forest structure and the accessibility of food resources for birds). Comparative studies of foraging behavior among forests with different plant species and structure indicate that differences in forest composition are associated with bird species densities (Maurer and Whitmore 1981, Franzreb 1983, Sabo and Holmes 1983).

Our data on bird foraging behavior and microhabitat use have important implications for

bird conservation and management in the coastal woodlands of Buenos Aires Province. *Ligustrum lucidum* is an invading exotic in these woodlands (Ribichich and Protomastro 1998), and surrounding the El Destino Reserve are patches of dead native woodland under a continuous cover of this fast-growing tree (A. M. Ribichich pers. comm.). Control of this exotic species should be a priority for management of El Destino. At the same time, efforts to regenerate old growth features (such as canopy height and tree species composition) in disturbed woodlands may be crucial for conservation of bird populations in coastal woodlands of eastcentral Argentina.

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FOOD AND PREDATION RISK AS FACTORS RELATED TO FORAGING LOCATIONS OF NORTHERN FLICKERS

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ABSTRACT.—Foraging site selection by birds may be related to foraging efficiency, food availability and abundance, and predation risk. We identified selectively used foraging habitat within home ranges of 29 adult radio-tagged Northern Flickers (*Colaptes auratus*) in British Columbia during the nestling period. We compared habitat characteristics of flicker foraging locations to randomly selected locations in their home range using discriminant function analysis. Foraging plots were located in grassland and were characterized by a lack of tall vegetation, a large percentage of bare ground, and a high density of small anthills. Foraging plots had five times more anthills than random plots. Foraging plots also were closer to trees and forest edges than random plots. The random plots had significantly more medium and tall vegetation than foraging plots, and litter (dead grass) was the most abundant type of cover. Mortality of adult flickers attributed to avian predation while foraging was 14% during 1999 and 3% during 2000. The sparse ground cover of foraging plots likely increased access to food, whereas foraging near trees likely decreased avian predation. The marked selectivity of foraging areas by flickers suggests that foraging ability could be negatively affected by land use practices that alter the structure of ground cover. *Received 3 October 2001, accepted 6 June 2002.*

Foraging behavior of birds is influenced by time and energy spent searching for and handling prey, as well as the energetic content of food (MacArthur and Pianka 1966, Schoener 1971, Stephens and Krebs 1986). For central place foraging birds, which initiate and end foraging trips from and to the same location (e.g., a nest), the cost of foraging also may include increased predation risk and increased time and energy expenditure the farther the distance traveled from the nest to the foraging site (Johnson and Swihart 1989). Foraging animals generally should try to maximize rate of energy gain and minimize costs of foraging and predation risk (Krebs 1980). The selection of a foraging location, therefore, should be based on perceived predation risk, food abundance and availability, foraging efficiency, and intraspecific or interspecific competition (Gamboa and Brown 1976, Eiserer 1980, Lima and Dill 1990, Giesbrecht and Ankney 1998, Rolstad et al. 2000).

Several studies of ground-foraging birds have implicated predation risk, food abundance, or food availability as important determinants of foraging location; however, these relationships are complex. For example, Dark-eyed Juncos (*Junco hyemalis*), House Sparrows (*Passer domesticus*), and White-crowned Sparrows (*Zonotrichia leucophrys*) foraged at feeders closer to tree cover when given a choice, and shifted to farther feeders as food became depleted near tree cover (Schneider 1984, Giesbrecht and Ankney 1998). In another study, however, three species of ground-feeding sparrows experienced a trade off between foraging too close to protective cover, which may harbor predators, and foraging too far away from cover to escape from an attacker (Lima et al. 1987). Foraging in tall vegetation can provide better cover from avian predators but also may impede movement and impair foraging efficiency as well as decreasing detection distance of predators. Shorter vegetation may result in greater exposure to predators but allow a quicker detection rate and greater foraging efficiency (Roth 1979, Eiserer 1980, Ostrand et al. 1996). For example, Brown-headed Cowbirds (*Molothrus ater*) foraged in short grazed grasslands where invertebrate density was greater than in tall vegetation, although their vigilance in the former type of habitat also was highest (Morris and Thompson 1998). Presumably, combinations or trade offs among multiple factors such as food abundance, distance traveled, and predation risk yields the optimal solution for a choice of foraging patch (Covich 1976).

Woodpecker species often have specialized diets and foraging habitat requirements (Williams 1975). During summer, most woodpeckers forage on ants and insect larvae that they

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obtain from crevices in trees or by removing bark and excavating holes in infected dead wood (Short 1982). Varying sizes, ages, or areas of the tree often are used by different woodpecker species or sexes within species (Kilham 1965, Jackson 1970, Williams 1975, Gamboa and Brown 1976, Conner 1980, Torgersen and Bull 1995, Fayt 1999). The Northern Flicker (*Colaptes auratus*) is a unique North American woodpecker because it forages almost exclusively on the ground during summer, specializing on ants and beetle larvae (Beal 1911, Cruz and Johnston 1979). The brownish barred plumage of the Northern Flicker also differs from the conspicuous black, white, and red coloration of most other woodpecker species, which suggests that predation risk during foraging may have favored cryptic plumage. However, there are no data on mortality rates of adults during breeding to assess levels of predation.

Flickers play a keystone role in many northern forest communities as the most active cavity nest excavators (Martin and Eadie 1999, Aitken et al. 2002), yet little is known about their habitat use while foraging. Habitat selection can occur on a hierarchal scale, from the choice of a home range on the landscape to the choice of a food item on a feeding site (Johnson 1980). Our goal in this study was to focus on selection of foraging habitat at the scales of feeding sites within home ranges, and food items within feeding sites. This was accomplished by comparing characteristics of foraging plots to random plots in the home range. We predicted that foraging sites would have a greater density of ants, the main prey of flickers, and that flickers would forage close to protective cover to minimize predation risk. Because no data exist on mortality rates of flickers associated with predation, we also analyzed the fate of the radio-tagged individuals.

METHODS

Study area and radio telemetry.—We conducted the research from May to July 2000 in central interior British Columbia near Riske Creek (51° 52′ N, 122° 21′ W). The study area encompassed about 200 km^2 of grassland with aspen (*Populus tremuloides*) groves, mixed forest (Douglas fir, *Pseudotsuga menziesii*; lodgepole pine, *Pinus contorta*; and aspen) and scattered lakes and ponds. Cattle grazed on the entire study area for a few weeks during May and September.

During mid-May, we trapped adult flickers at the nest during incubation and banded them with a unique combination of colored leg bands (see Wiebe 2001, Wiebe and Swift 2001). We aged birds as yearlings or adults (≥2 years) using molt criteria Pyle et al. (1997) and recorded sex. We attached radio transmitters (Holohil Systems Ltd., Ontario, BD-2G) weighing 1.8 g to the central rectrices of flickers using cyanoacrylate glue (Kenward 1987) and microfilament line. The radios represented approximately 1% of the body mass and therefore were unlikely to affect behavior (Cochran 1980, Wanless 1992, Wiktander et al. 2001). From a sample of about 80 breeding pairs that we banded, we arbitrarily selected 29 flickers (14 males, 15 females) for radio tracking, using only one individual per pair.

We radio tracked each flicker during 2.5-h sessions, which were rotated among three observers and three time periods: morning (07:00–11:00 PST), midday (11:00–14:00), and afternoon (14:00–18:00). Tracking sessions occurred 6–8 times for each bird, beginning when nestlings were about five days old, when they no longer required constant brooding, and continued until the chicks fledged about 20 days later. During tracking sessions, we marked the target bird's location every 30 min, which allowed us to delineate home range boundaries and identify locations where the bird was foraging. We obtained the locations by a visual sighting of the birds with binoculars from a distance in an attempt not to flush them. We marked the locations with flagging tape after the bird had left the area and recorded the UTM coordinates using a global positioning system. Due to difficulties in observing good foraging points during all 6–8 tracking sessions, we measured only 3–4 randomly selected foraging points per bird to weight the data from all individuals and all home ranges equally. To avoid sampling the same area of the home range repeatedly, we used only one foraging point per tracking session.

Characteristics of foraging and random plots.—We evaluated characteristics of foraging locations either immediately following the tracking session or within one week, in which case the areas were described in the field notes on the day of observation. At each foraging location, we assessed habitat characteristics in a 1-m^2 quadrat. We visually assessed the ground coverage (in %) of the following: bare ground, lichen, rock, cow dung, dead standing vegetation (litter), short (<10 cm tall) vegetation, medium (10–20 cm) vegetation, and tall (>20 cm) vegetation. Vegetation height categories were based on a flicker's height. We reasoned that flickers probably would be able to see over short grass while foraging but would have to stand in an upright position to see over medium vegetation, and may have a totally obstructed view in tall vegetation. We measured the proportions of rock and lichen since some ant species construct nests under rocks and lichen (Smallwood and Culver 1979) and we observed flickers probing in the soil around edges of rocks and flipping over pieces of lichen. We counted the number of small (<5 cm diameter) anthills in the quadrat to

TABLE 1. Habitat variables measured for foraging (n = 29) and random (n = 29) plots in home ranges of Northern Flickers, British Columbia, Canada, 2000. Normally distributed or transformed variables are reported as means or back-transformed means (95% lower confidence limit, 95% upper confidence limit), respectively. When variables could not be normalized, medians (lower (25%) quartiles, upper (75%) quartile) are reported.

Variable	Transformation[a]	Foraging plots	Random plots
Bare ground (%)	ND	22.8 (17.9, 27.8)	5.4 (3.7, 7.2)
Litter (%)	ND	14.6 (11.2, 17.9)	32.3 (27.3, 37.3)
Short vegetation (%)	ND	34.1 (30.0, 38.1)	23.0 (19.0, 27.0)
Medium vegetation (%)	ND	9.8 (8.1, 11.4)	17.0 (14.9, 19.1)
Distance to forest (m)	ND	54.8 (40.1, 69.5)	97.4 (86.2, 108.6)
Nearest tree (m)	ND	11.2 (9.0, 13.4)	17.2 (15.8, 18.6)
Distance to cow dung (m)	ND	4.5 (3.9, 5.0)	6.5 (5.6, 7.4)
Lichen (%)	A	9.7 (6.2, 14.0)	3.5 (1.8, 5.8)
Rock (%)	A	2.9 (1.8, 4.1)	0.9 (0.4, 1.4)
Tall vegetation (%)	A	1.4 (1.0, 2.1)	14.1 (10.9, 17.7)
Cow dung (%)	—	1.0 (0, 1.5)	1.0 (0, 1)
Number small anthills/m^2	—	5.0 (3.5, 6)	1.0 (0, 1.5)
Number of large anthills	—	0.0 (0, 1)	0.0 (0, 0.5)

[a] Transformations applied to data to achieve normality: A, arcsine square root; —, transformation unsuccessful; ND, normal distribution without transformation.

obtain small anthill density. Small anthills were easily visible on bare ground and in short vegetation, but we also looked for them on the ground under taller vegetation and litter, which can accumulate to a depth of about 15 cm.

We measured the distance from the center of the quadrat to the nearest tree within 20 m. We chose 20 m as the limit for tree cover because trees farther than 20 m from a foraging location probably would not provide protection in the event of a surprise attack from an avian or mammalian predator. We measured the distances to the nearest five productive cow dung pats within 20 m and we calculated the mean value for each quadrat. We considered cow dung productive if it contained items such as eggs, pupae, larvae, or adult ants or beetles, therefore providing an available food source for flickers. Also, we counted the number of large (15–30 cm diameter) anthills within 20 m of the foraging plot and estimated the distance to the nearest forest edge.

We compared foraging plots to random plots, selected to represent available grassland habitat within each home range. For each foraging plot, we used a random numbers generator to establish two plots at random distances from the nest but within the home range boundaries. One plot was established at a random direction determined by a blind twist of the compass dial while the other was placed in the same direction as the foraging plot being measured. We did not establish any random plots in the forest because we rarely observed flickers foraging there, and all foraging plots were located in grassland or edge (≤20 m from forest) habitats. We used identical methodology to assess characteristics of random and foraging plots, and we measured random plots at the same time as the corresponding foraging plot.

Data analysis.—For analysis, we used the mean values of each variable for the 3–4 foraging plots and 6–8 random plots in each home range of each individual for a total of 29 foraging plots and 29 random plots. We tested habitat variables for normality using a one-sample Kolmogorov-Smirnov test at the 95% confidence level (Zar 1999), and transformed variables when necessary (Table 1). We used two-sample t-tests to compare variables that the multivariate analysis suggested were important.

Because the ground cover variables sum to 100%, we excluded lichen from the multivariate analyses to avoid statistical redundancy. Therefore, we entered 12 habitat variables into two multivariate ordination techniques. We performed principal component analysis (PCA) to explain the greatest percent of total variance in the variables (Tabachnick and Fidell 1983). A scree test, a plot of the variance associated with each component, was generated in PCA to determine the number of components to consider in the analysis. Subsequently, we used stepwise discriminant function analysis (DFA) to identify the subset of variables most effective at discriminating between random and foraging plots and to determine their success at predicting correct plot classification (Tabachnick and Fidell 1983). We also compared foraging plot characteristics between sexes using DFA. A correlation matrix was used in the DFA and PCA to standardize the variables measured in different scales. A variable was entered into the DFA model if the probability level of its F value was <0.05 and was removed if it was >0.10.

Fate of radio-tagged flickers.—During tracking sessions, we visually located the birds so we were able to confirm whether the bird was alive, dead, or lost. If the bird was found dead, we assessed whether it was eaten by a mammal or avian predator by the condition of the carcass and the way the feathers had been plucked or chewed. Although we relocated birds every

2–3 days during the brood-rearing period, we could not eliminate the possibility that the bird had initially died of natural causes or disease, and was scavenged later. Since we placed radio transmitters on birds during early incubation and began radio tracking when chicks were about 5 days old, there was a ≥10-day adjustment period for the birds with the radio transmitters. Since no birds died during this period, we assumed that mortality was not a direct result of radio tagging.

We considered a bird lost if the signal was not detected within the study area or if the radio came off the bird. Lost birds (n = 17) were never detected again, so they were not included in the mortality estimate because we had no knowledge of their fate. Also, since there were no cases where a radio-tagged bird was not detected and then later found (i.e., no detection failures), we defined mortality rate as the number of radio-tagged birds found dead divided by the total number of birds radio tagged (excluding lost birds) × 100 during the brood-rearing period, approximately 24 to 27 days. This estimate is therefore not representative of mortality rate during the summer, but during the time adults have chicks in the nest.

RESULTS

Characteristics of foraging and random plots.—Short vegetation and bare ground were the most abundant types of ground cover in foraging plots whereas tall vegetation was the least common (Table 1). In the random plots, litter was most abundant whereas rock, lichen, and bare ground made up only a small percentage of cover (Table 1).

There were five times more small anthills in foraging plots than in random plots (Mann-Whitney U = 32.0, n = 58, $P < 0.001$; Table 1). All foraging plots contained at least one small anthill (range = 1–21, median = 5). Random plots had a median of one anthill and often contained none. We found no evidence of probe marks indicating flicker foraging in any of the random plots. In contrast, the ground in the foraging plots usually had multiple probe marks and soil or lichen turned over with ants scattered over the surface, sometimes carrying larvae, pupae, or eggs. Foraging plots also often had numerous probe marks around the edges of rocks, under which were ant colonies.

Random plots were twice the distance to forest edge as were foraging plots (two-sample t = −4.723, df = 56, $P < 0.001$; Table 1). Foraging plots were a mean distance of 11 m from the nearest tree compared to 17 m for random plots (two-sample t = −4.735, df = 56, $P < 0.001$; Table 1).

Two components were considered in the PCA based on a break in the slope of a scree test. Together, PCA axes 1 and 2 explained 49.4% of the variance with axis 1 alone explaining 34.1% (Fig. 1). Greater numbers on PCA 1 represented increases in the density of ground cover. Bare ground and number of anthills were highly negatively correlated with axis 1 and associated with foraging plots, whereas litter and tall vegetation were highly positively correlated with axis 1 and associated with random plots (Fig. 2). PCA 2 appeared to measure distance to cover; positive values indicated a long distance to a tree or forest edge (Fig. 2). Overall, foraging and random plots were distinct as shown by the small overlap between the groups on the scatterplot (Fig. 1).

Using DFA to distinguish plots.—The DFA retained five variables as potential discriminators of foraging and random plots ($P < 0.001$; Table 2), while the other nine were statistically redundant and discarded. Density of small anthills was the strongest discriminating variable between foraging and random plots (Table 2). Tall grass also was important, with random plots having taller vegetation than foraging plots. Foraging plots also could be distinguished by having more bare ground, being closer to forest edges, and closer to a tree (Tables 1 and 2). The discriminant function of the entire data set had an overall classification success of 98.3%. No variables were kept in a DFA model testing for differences in foraging plots between males and females, indicating that characteristics of foraging areas did not differ significantly between the sexes.

Predation on radio-tagged flickers.—Although we did not observe any radio-tagged flickers being killed by predators during tracking sessions, we found the remains of radio-tagged birds both in and away from the nest. We saw flickers being chased by Cooper's (*Accipiter cooperii*) and Sharp-shinned (*A. striatus*) hawks. We observed coyotes (*Canis latrans*), red foxes (*Vulpes fulva*), martens (*Martes americana*), fishers (*Martes pennanti*), longtail weasels (*Mustela frenata*), and minks (*Mustela vison*) during the study, but they were not stalking birds.

During 1999, one male and three females

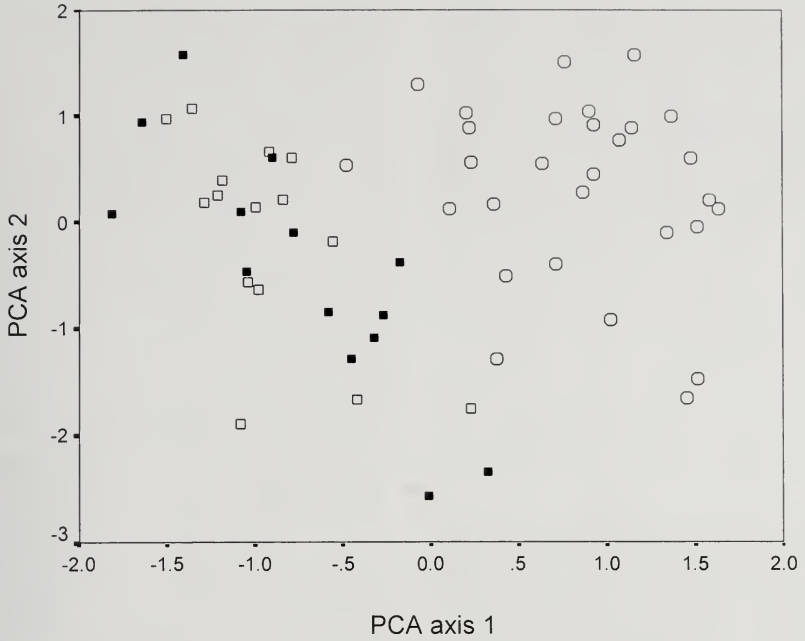

FIG. 1. Scatterplot of PCA scores for random (circles) and foraging (squares) plots within home ranges of 29 Northern Flickers, British Columbia, Canada, 2000. Foraging and random plots show little overlap whereas foraging sites used by males and females (open and filled symbols, respectively) overlap extensively. The structure of each PCA axis is illustrated in Fig. 2.

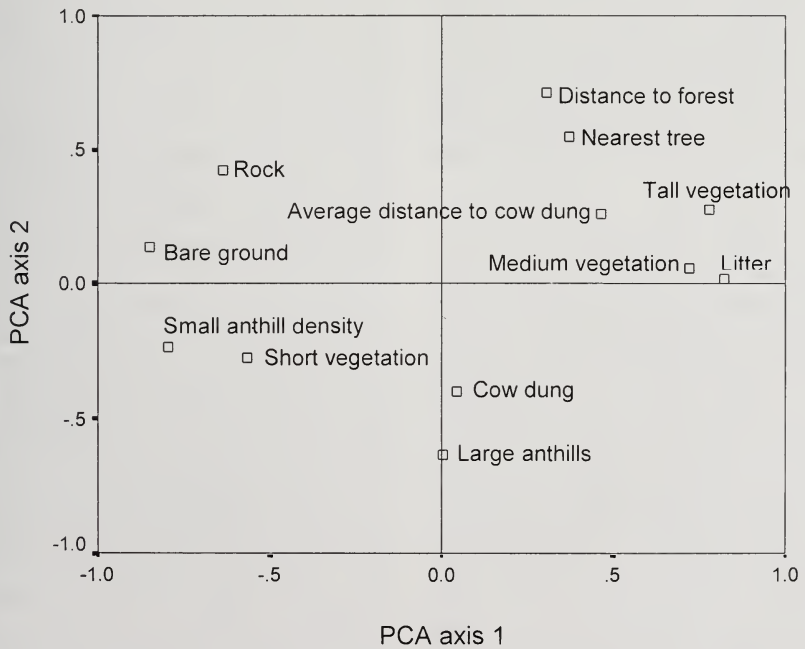

FIG. 2. Plot of component loadings of the habitat variables on the first two axes in principal component analysis after varimax rotation. Habitat variables were measured in foraging and random plots of home ranges of Northern Flickers in British Columbia during the breeding season of 2000. Axis 1 represents mainly ground cover whereas axis 2 is influenced strongly by distance to protective cover such as trees or forest.

TABLE 2. The subset of variables from Table 1 retained by a discriminant function analysis as the most important to distinguish between foraging and random plots. Foraging and random plots were located in 29 home ranges of Northern Flickers in British Columbia in 2000. Positive signs for the pooled within group correlations show that the variable was positively correlated with random plots and negative signs indicate negative correlations with foraging plots.

Habitat variable	Correlation coefficient
Small anthill density	−0.539
Tall vegetation	0.501
Bare ground	−0.472
Distance to forest	0.424
Nearest tree	0.374

(14% of 28 birds) were eaten by what we concluded to be an avian predator. During 2000, one female was eaten by an avian predator (3% of 31 birds). We found plucked feathers from these birds in grassland areas or among small, scattered conifer trees near forest edges. Attacks in these cases likely were made while the flickers were foraging, as avian predators probably would not enter nest cavities. In addition to the flickers eaten by avian predators, one male was found in 1999 cached in grass under a tree, and another male was cached in a mustelid den in 2000. This represents mortality rates of 18% in 1999 and 6% in 2000 for an approximate 27-day brood-rearing period.

DISCUSSION

Food abundance and food sources.—Within their home ranges, flickers were highly selective in their use of foraging sites (Fig. 1). DFA indicated a selective use of grassland areas with small anthills and greater percentages of bare ground (Table 2). The fact that anthill density was the best discriminating variable suggests that food abundance may be the most important variable determining foraging location. The small anthills upon which flickers foraged occurred only in areas with short vegetation and bare ground, so it is likely that these variables are related. We did not find small anthills under tall vegetation, although a few anthill mounds (5 cm diameter) that were built with small pieces of grass emerged on top of the litter, and disturbance to these caused ants to swarm. Flickers foraged on these grass anthills occasionally.

Foraging flickers occasionally were flushed from the ground in an area lacking anthills, probe marks, or other soil disturbance but with ants that were walking along ant trails. We never observed flickers eating ants (mainly of the genus *Formica*) directly off large (usually 15–30 cm diameter) mounds, although they ate traveling *Formica*. Green Woodpeckers (*Picus viridis*) also have been observed feeding along ant trails during summer (Rolstad et al. 2000). *Formica obscuripes* (thatch ants) aggressively defended their nest mounds and swarmed objects placed near or on their nests, biting with their large mandibles and spraying formic acid (Hölldobler and Wilson 1990; CLE unpubl. data). This behavior may deter flickers from foraging on these mounds and explain why large anthills were not an important factor in foraging location. Ants such as *Lasius* spp. and *Tapinoma sessile* that occur in the smaller anthills and under rocks were less aggressive and ran around erratically when disturbed, probably making them more vulnerable to the foraging birds.

Even though cow dung was closer to foraging sites than random sites, it did not strongly predict the location of feeding sites (Table 1). Cow dung, which on our study site contained invertebrates such as *Lasius* and *Mirmica* ants (adults, larvae, pupae, eggs), as well as Coleoptera and unknown larvae, can be used by invertebrates for >30 days in temperate regions and can take as long as 340 days to fully degrade (Floate and Gill 1998, Moeed et al. 1993). Although insects within cow dung seemed to be an important food source for flickers, especially on rainy and cold days when ants were not active on the ground surface, dung pieces were abundant and appeared uniformly distributed across the grassland with varying species and stages of invertebrate development.

Food availability and energetic costs of locating prey.—Flickers selectively used short grass and bare ground because ants probably were more accessible there. Since we found very few anthills in tall grass, the patches flickers selected for foraging had both a greater abundance and availability of prey. Rolstad et al. (2000) found three times greater overall biomass of ants in meadows and pastures than

in forests or clearcuts. Grazed areas tended to have greater invertebrate densities than ungrazed areas (Morris and Thompson 1998). Not only are insects more abundant and vulnerable on bare ground, but probing for subterranean larvae and pupae also would be easier in soil than in thick vegetation. In tall grass, both Northern Mockingbirds (*Mimus polyglottos*) and American Robins (*Turdus migratorius*) were forced to adopt alternative feeding styles such as using aerial perching or plucking small insects off grass strands, respectively, rather than gleaning larger insects from the soil surface (Roth 1979, Eiserer 1980). This reduced the feeding efficiency for both species. Mourning Doves (*Zenaida macroura*) avoided tall and dense vegetation and selectively foraged in areas with bare soil and short scattered vegetation when food was experimentally provided equally in both areas, probably because food was more difficult to detect in tall vegetation (Ostrand et al. 1996).

Tall or dense vegetation also may impede or alter movement of ground-foraging birds not equipped to move through it. American Crows (*Corvus brachyrhynchos*) avoided tall, dense vegetation because it probably was difficult to move through on foot (Sugden and Beyersbergen 1987, Sullivan and Dinsmore 1992). Movement of robins also was hindered by tall grass and changed their behavior from running or walking in short vegetation to hopping in tall vegetation (Eiserer 1980). Since flickers move along the ground by hopping and occasional running, taller vegetation may make locomotion more difficult and energetically costly.

Sex differences in foraging sites.—Woodpecker species that forage in trees, such as Downy (*Picoides pubescens*), Hairy (*P. villosus*), or White-backed (*Dendrocopus leucotos*) woodpeckers, often exhibit intrasexual differences in resource use, probably in order to avoid intraspecific competition (Jackson 1970, Gamboa and Brown 1976, Aulén and Lundberg 1991). In our study, the lack of differences between foraging sites of male and female flickers may be related to the similar size and morphology of the sexes (Wiebe 2000), their narrow diet range, and the homogenous structure within grassland foraging patches. It is more difficult for ground-foraging birds, which are restricted to foraging in a horizontal plane, to partition the habitat or develop different foraging niches between sexes (Recher and Holmes 2000). Abundance of ants in patches on the ground also may be great enough that little intraspecific competition occurs and therefore different foraging strategies have not evolved. Male and female flickers foraged together without agonistic behavior and often near other insectivorous ground-foraging birds (Elchuk 2002).

Predation risk and distance to cover.—Avian predation may be an important factor in determining flicker foraging behavior, the location of feeding sites, and plumage color. The 12% mortality rate of flickers (mean for two seasons; $n = 7$ of 59 birds), is comparable to the 15% mortality rate found for Pileated Woodpeckers (*Dryocopus pileatus*) killed by Northern Goshawks (*Accipiter gentilis*) in Alberta during three breeding seasons ($n = 5$ of 33 birds; Bonar 2001). In addition to the Sharp-shinned and Cooper's hawks we observed, the Northern Harrier (*Circus cyaneus*) and Broad-winged Hawk (*Buteo platypterus*) also prey on flickers (Moore 1995). The ground-foraging Green Woodpecker in Italy is one of the main prey items of the Lanner Falcon (*Falco biarmicus*; Morimando and Pezzo 1997), whereas flickers make up 34% of the diet of Northern Goshawks in Wyoming (Squires 2000). Götmark and Unger (1994) suggested that the bright red, black, and white colors of many tree-foraging woodpeckers were aposomatic. However, ground-foraging woodpeckers such as the Northern Flicker and Green Woodpecker lack these conspicuous colors and are cryptic against the background where they forage (Short 1982). Ground-foraging birds also may be easier for predators to attack than tree-foraging species (Selås 1993).

Although different predators may have different attack strategies, foraging flickers chose sites closer to trees and forest edges (Tables 1 and 2) suggesting that these areas were safer. This conclusion is supported by observations in the field of flickers flying to nearby trees when flushed by observers or when an avian predator flew overhead. After scanning for a few minutes, they flew to the forest or dropped back to the ground to resume foraging. This use of protective vegetative cover also has been observed in other grassland

birds such as the Yellow-billed Magpie (*Pica nuttalli*), American Robin, Brewer's Blackbird (*Euphagus cyanocephalus*) and European Starling (*Sturnus vulgaris*) when a predator appears or upon hearing an alarm call (Verbeek 1964, 1972). Using areas with shorter vegetation also may enhance detection of predators and aid in early escape (Ostrand et al. 1996). Early detection may be important for flickers, which did not give alarm calls while foraging despite occurring in foraging flocks with conspecifics and other species.

In summary, we found that Northern Flickers were highly selective of ground cover characteristics within the grassland portion of their home ranges. Quantifying energy demands of adults and the rate of energy gain from foraging patches is needed to determine whether high quality foraging areas are limiting flicker reproduction and population densities. Our study suggests that, in addition to the management concern over retaining appropriate nest trees for woodpeckers on the landscape, attention should be given to characteristics of grassland at a microhabitat scale, and grazing practices that may alter it.

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ANNUAL SURVIVAL OF ADULT AMERICAN REDSTARTS AND OVENBIRDS IN THE SOUTHERN BOREAL FOREST

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ABSTRACT.—Using constant effort (1993–1996) and playback mist netting with color banding (1996–1999), we estimated annual survival rates of Ovenbirds (*Seiurus aurocapillus*) and American Redstarts (*Setophaga ruticilla*) at four sites in the boreal forest of central Saskatchewan. For both species, the model that best described our data included a residency index that differentiated individuals caught more than once within the breeding season of initial capture (residents) from individuals caught only once (transients). Transients had considerably lower recapture rates than residents. The residency index was a more effective means of addressing violations of the homogeneity of capture assumption inherent in Cormack-Jolly-Seber models than a two-stage or age-structured model. We detected no significant differences in survival or recapture rate of male Ovenbirds between constant effort and playback mist netting techniques, although our estimate of annual survival for male Ovenbirds captured using playback (0.62 ± 0.06 SE) was higher than when we used constant effort netting (0.44 ± 0.13 SE). We observed no significant differences in survival between male (n = 99) and female (n = 113) American Redstarts or between second-year (n = 50) and after-second-year (n = 49) American Redstart males (overall survival = 0.55 ± 0.09 SE). For Ovenbirds, the model that best fit the data incorporated sex specific differences in survival with females (n = 76) having lower survival (0.21 ± 0.09 SE) than males (n = 197, 0.60 ± 0.12 SE). Without accounting for the presence of transient birds in our models, our estimates of survival would have been unrealistically low. Residency indices based on the number of times an individual was captured within a season seem to provide an effective means to account for transients. *Received 27 November 2001, accepted 15 July 2002.*

An apparent decline of some North American passerine populations has stimulated considerable research into the factors influencing songbird populations (Holmes et al. 1996, Porneluzi and Faaborg 1999). Most research has focused on how habitat or landscape features are related to population density and nesting success (e.g., Donovan et al. 1995, Robinson et al. 1995). Less is known about adult and juvenile survival, although precise estimates of these life history parameters are key in creating realistic demographic models for use in conservation and management.

Constant effort netting is a common method used to capture passerines and estimate survival (DeSante and Burton 1994). Constant effort netting is limited by the problem that previously banded individuals are not always recaptured even though they are alive (Chase et al. 1997). Imperfect recapture histories can be caused by permanent dispersal from sites, which cannot be distinguished from mortality, or temporary dispersal from sites whereby individuals are alive but not captured each year they are alive. To account for temporary dispersal, methods such as Cormack-Jolly-Seber (CJS) models have been used to correct survival estimates based on recapture rate.

The main assumption of CJS models is that marked individuals in the population have an equal probability of being recaptured (Lebreton et al. 1992). Constant effort netting can result in the capture of transient individuals who after initial capture are never seen again (i.e., migratory or individuals that are not territorial), violating the homogeneity of capture assumption (Chase et al. 1997, Bertram et al. 2000, Sandercock and Jamerilo 2002). To analyze data for which the homogeneity of capture assumptions were not met, some studies have used a residency index, whereby individuals captured at least twice within the same breeding season are treated as residents and individuals captured only once within a breeding season are assumed to be transients (Chase et al. 1997). A potential difficulty with this approach is the possibility that residents are captured only once and thus are incorrectly classified (Nur et al. 1999). Other studies allow for heterogeneous recapture rates among marked individuals by structuring CJS models into two stages such that survival and recapture in the year after marking differ from sur-

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vival estimated over subsequent time periods (Pradel et al. 1997, Bertram et al. 2000). The main assumption of the two-stage approach is that individuals captured multiple times in future years are likely to be residents while individuals never seen again are more likely to be transients. This approach accommodates the possibility that some individuals captured only once within a season actually are residents. A final alternative has been to color mark individuals and utilize the capture history of only those individuals known to breed on the study area (Nur and Geupel 1993). Although all these techniques have been widely used, the relative effectiveness of these modeling strategies as a means of assessing survival of passerines rarely has been tested (Nur et al. 1999).

Here we report survival and recapture rates from four years of banding adult American Redstarts (*Setophaga ruticilla*) and Ovenbirds (*Seiurus aurocapillus*) from sites in the boreal forest of central Saskatchewan. Little is known about the demography of forest birds in this northern region. Given the vast size, the high diversity of birds, and the rapid pace of anthropogenic change in the boreal forest, studies are needed that document basic demographic parameters for birds in this area. Our objectives were to (1) generate estimates of survival in the presence of transient birds and determine if residency indices, two-stage models, or a combination of both methods were more parsimonious explanations for our data; (2) compare survival and recapture rates from Ovenbirds captured by constant effort mist netting versus a detailed population study using playback netting and color banding; and (3) determine if we could detect differences in survival or recapture rates among different sex and ages classes of both species.

METHODS

Study area.—We conducted field work on four study sites in Prince Albert National Park (53° 50′ N, 105° 50′ W), located in northcentral Saskatchewan (Bouman et al. 1996). Prince Albert National Park is a 387,500-ha protected area surrounded by agricultural land to the south and commercial forests with active forest harvesting on the other three sides. We sampled two sites from 1993–1996. Site 1 was a mature (70 years) trembling aspen (*Populus tremuloides*) forest with a 20- to 25-m canopy and a 2- to 3-m shrub layer of beaked hazelnut (*Corylus cornuta*). Site 2 was an old (100 years) mixed wood forest with 40% white spruce (*Picea glauca*) and 60% trembling aspen in the canopy (25–30 m high). The understory at this site was relatively diverse with a variety of shrubs, including balsam fir (*Abies balsamifera*), white spruce, green alder (*Alnus crispa*), and beaked hazelnut. We sampled two other sites from 1996–1999. Site 3 was an old aspen forest, with a shrub layer dominated by green alder. Site 4 was an old mixed wood forest with 30% white spruce and 70% trembling aspen. Sites were ≥10 km apart, ≥1 km from the edge of the park boundary, and were surrounded on all sides by forest of a similar type.

Capture methods.—We conducted constant effort mist netting at sites 1 and 2 from June 1 through July 31, 1993–1996. Net lanes were placed along permanently established 2- to 4-m wide trails. Each lane consisted of 10 nets (12 m × 2 m, 36-mm mesh) spaced 10 m apart and alternated on opposite sides of a trail. We opened nets at 06:00 CST and monitored them for 6 h daily for two days per sampling period at each site. On the second day, we moved the lane so that the first net of the second day was 10 m farther along the trail than the last net of the first day. The number of monitoring periods ranged from 2–4 times per month with each monitoring period separated by a mean of 10 days. All recapture histories from constant effort mist netting were derived from physical captures, as none of these birds were color banded.

At sites 3 and 4, we placed two nets in a V shape and used playback to lure male Ovenbirds into nets. After capturing a bird, we moved the nets to the next territory until all males were captured or visually sighted to determine their banding status. We banding during June and early July, 1996–1999. We searched each 25-ha site (flagged cells, 50 m × 50 m) ≥3 times per year for marked birds (Bayne and Hobson 2002).

All birds captured at sites 1 and 2 received a USFWS numbered aluminum band. At sites 3 and 4, we also used plastic color bands to give each individual a unique band combination. We banded only during the breeding period, so we were able to determine the sex of all adult birds based on the presence of a brood patch or cloacal protuberance (Pyle et al. 1987). We aged individuals as either hatch-year (HY) or after-hatch-year (AHY) based on skull ossification and plumage characteristics (Pyle et al. 1987). HY birds were excluded from analysis. We aged male American Redstarts as second-year (SY) or after-second-year (ASY) based on plumage characteristics (Pyle et al. 1987).

Survival estimation.—We estimated annual survival (ϕ) and recapture (p) rates using methods described in Lebreton et al. (1992). Using program MARK (White and Burnham 1999), we fit CJS models to the data and used them to create maximum likelihood estimates for survival and recapture rates. Model selection within each candidate model set was assessed for plausibility using Akaike's Information Criterion corrected for small sample size (AIC_c; Burnham and Anderson 1998). The model from each model set with the lowest

AIC_c was considered the most parsimonious explanation for the data. Comparisons of models within the candidate model set were based on an index of relative plausibility using normalized Akaike weights and the difference in AIC_c scores between models (Burnham and Anderson 1998).

To determine if it was necessary to account for transients when modeling the data from constant effort mist netting, we compared the fit of four models. Model 1 included a residency index in both the survival and recapture terms, whereby individuals captured more than once during different sampling periods within the same breeding season were classified as residents and individuals captured only once within the breeding season were considered transients (*sensu* Chase et al. 1997). In model 2, we used a two-stage structure to allow for differential survival and recapture between the year after marking and all subsequent periods (Pradel et al. 1997). This model is structurally analogous to models that account for age differences in survival between the first and second year of banding (Lebreton et al. 1992). The third model was a combination of model 1 and 2. We assumed the survival and recapture of transients was different than that of residents, but only in the year after initial capture. We assumed that "transients" that returned ≥2 years after initial capture had survival and recapture rates similar to those of residents (i.e., these birds likely held territories near the net lane but only happened to be captured once in the year of initial capture; Nott and DeSante 2002). We compared these models to a null model, where we assumed that all individuals had the same survival and recapture rate. We created each model set separately for each species. All individuals regardless of sex and age were pooled in these analyses.

To assess whether our estimates of survival and recapture rate of male Ovenbirds differed based on method of capture, we compared the fit of four other models. In model 1, we assumed the survival and recapture rates of male Ovenbirds differed based only on how they were captured (constant effort or playback). In model 2, we compared the survival and recapture rates of male Ovenbirds estimated from the different capture methodologies while accounting for transients. The transient model used in this model set included the residency index only (see results). In model 3, we assumed the survival and recapture rates of male Ovenbirds did not differ between techniques but that it was important to account for transient individuals. We compared these models to a null model that assumed that there were no differences between capture methods and that accounting for transients was unnecessary.

Finally, we determined whether or not we could detect differences in the survival or recapture rates of different sex and age classes while accounting for the presence of transients using the residency index (see results). For American Redstarts, we began with a model that included male age (SY or ASY), sex, and the residency index. As we did not have *a priori* hypotheses about how age and sex might interact with the residency index, we chose to use an all possible subsets approach to model these data (Kleinbaum et al. 1988). Using the approach outlined in Lebreton et al. (1992), we generated eight models that varied the different combinations of age, sex, and residency status for recapture rate. After generating the most parsimonious model in terms of recapture rate, we generated eight more models that varied these terms for survival. We used a similar approach for Ovenbirds, except that we did not include age of males in our models. We decided *a priori* not to include site or year in any of our analyses because of limited sample sizes within years and because the actual years Ovenbirds were monitored differed among capture methodologies. In addition, most (98%) American Redstarts were captured at site 1. Previous analyses indicated no detectable difference between sites 3 or 4 or between years at these sites in the survival or recapture rates of male Ovenbirds (Bayne and Hobson 2002).

To assess the generality of our results relative to previous studies, we generated a data set of published return rates and survival estimates for American Redstarts and Ovenbirds from various wintering and breeding locations. We selected studies from a search of the Biological Abstracts data base, 1980–2002, using the search terms "return" or "survival" and "redstart" or "ovenbird." We also used those studies listed in the literature cited of those papers. We classified each study based on the method of estimation (corrected survival estimate or simple return rate), method of capture and recapture (constant effort or color banding), and sex-age class (all sex-age class combined, SY male, ASY male, AHY male, and AHY female). No estimates of juvenile survival were included in this analysis. We entered these factors as main effects in a generalized linear model that assumed a Gaussian distribution. We assessed the significance of the main effects using a Wald test. Several studies reported survival-return estimates from different sex, age, and habitat classes. To account for potential nonindependence of the survival-return rate estimates from the same study, we used a robust cluster technique in the program STATA (StataCorp 2001). This approach reduces the effective sample size to the level of the cluster, resulting in inflated standard errors that provide valid statistical inference if samples within the cluster are not independent. We assumed return rate and survival estimates generated from different study areas within the same paper were independent (i.e., Jamaica and New Hampshire; Holmes and Sherry 1992).

RESULTS

Accounting for transients.—Between 1993 and 1995, we captured and released 212 adult American Redstarts (99 males and 113 females), and 37 returned at least once in a subsequent year (Table 1). Of the total sample, 43 were recaptured within the same breeding season and were classified as residents (25 males

TABLE 1. Reduced array for American Redstarts and Ovenbirds showing the number of marked and recaptured birds occurring in Prince Albert National Park, Saskatchewan, Canada. Numbers are pooled among banding sites. Constant effort mist netting was used from 1993 to 1996 while playback netting was used from 1996 to 1999. R_i is the number of marked individuals released in year i, including newly marked and previously marked individuals (i.e., in year 2, 75 American Redstarts were released with 59 individuals newly marked in that year along with 16 birds that were recaptured from year 1). Annual values are the number of individuals from a given release cohort that were first recaptured in that year.

Species	Year	R_i	Year 2	Year 3	Year 4	r_i[a]
American Redstart (constant effort)	1	111	16	4	2	22
	2	75		15	1	16
	3	61			7	7
	m_j[b]		16	19	10	
Ovenbird (constant effort)	1	57	8	2	0	10
	2	45		5	1	6
	3	49			5	5
	m_j[b]		8	7	6	
Ovenbird (playback)	1	52	20	4	2	26
	2	79		27	7	34
	3	57			23	23
	m_j[b]		20	31	32	

[a] The total number of individuals from a release cohort captured at least once.
[b] The total number of recaptures in a given year.

and 18 females). The model with the residency index was a far more likely explanation of the data than the null (Δ AIC_c = 29.5), two-stage (Δ AIC_c = 32.5), or combined model (Δ AIC_c = 6.2). Based on the null model, the survival rate was 0.40 ± 0.07 SE while the recapture rate was 0.37 ± 0.10 SE. The model containing the residency index generated similar survival estimates for residents (0.55 ± 0.08 SE) and transients (0.44 ± 0.15 SE), but very different recapture rates (0.68 ± 0.13 SE and 0.16 ± 0.08 SE, respectively).

Using data from constant effort netting only, we captured 136 Ovenbirds (60 males and 76 females) between 1993 and 1995, and 19 returned to the same site in at least one year (Table 1). Twenty Ovenbirds (11 males and 9 females) met our criteria for classification as residents. The combined model was the most parsimonious explanation of the data and was far better than the null (Δ AIC_c = 7.9) or two-stage model (Δ AIC_c = 10.9). However, the combined model was no better than the model that included the residency index (Δ AIC_c = 0.2; Table 2). Based on the null model, the survival rate was 0.32 ± 0.11 SE and recapture rate was 0.38 ± 0.16 SE. The parameter estimates derived from the model with the residency index indicated residents and transients had similar survival rates (0.33 ± 0.09 SE and 0.43 ± 0.19 SE, respectively) but different recapture probabilities (1 and 0.18 ± 0.11 SE, respectively).

Constant effort versus playback.—Using playback, we captured 137 male Ovenbirds from 1996 to 1998 and 61 returned in at least one year (Table 1). Of these individuals, we believe four were transients that left their initial capture location during the breeding season. Male Ovenbirds captured by playback netting had a survival rate of 0.62 ± 0.06 SE and a recapture rate of 0.59 ± 0.08 SE. Males captured by constant effort mist netting had a survival rate of 0.44 ± 0.13 SE and recapture rate of 0.43 ± 0.17 SE. However, the model that provided the best fit to these data suggested no significant difference in survival or recapture rates for Ovenbirds caught using different capture techniques if transients were accounted for in the model (Table 2). Assuming no differences caused by capture method, we found that the recapture rate of transient male Ovenbirds (0.20 ± 0.13 SE) was considerably lower than that of residents (0.62 ± 0.07 SE), but that survival rates were not significantly different (0.55 ± 0.24 SE and 0.61 ± 0.05 SE, respectively).

Sex and age differences.—The model with the best fit to the American Redstart data incorporated constant survival (ϕ) for all sex-age-residency groups, with differences in the recapture rate (p) for resident and transient

TABLE 2. Summary of models comparing fit of different age and sex parameters as factors influencing survival and recapture rate of American Redstarts and Ovenbirds in Prince Albert National Park, Saskatchewan, Canada. Models are sorted by their AIC_c value, with the most parsimonious model listed first. The symbol ϕ indicates the survival rate while p is the recapture rate. Subscripts on model terms refer to different factors incorporated in the model (s = sex, r = residency status, a = age, and '.' = constant).

Model	AIC_c	ΔAIC_c	Akaike weight	Number of parameters	Deviance
American Redstart					
$\phi_{.}p_{sr}$	244.4	0.0	0.35	5	38.2
$\phi_{s}p_{sr}$	245.7	1.3	0.19	6	37.3
$\phi_{r}p_{sr}$	246.0	1.6	0.16	6	37.6
$\phi_{a}p_{sr}$	246.5	2.1	0.13	6	38.1
$\phi_{sa}p_{sr}$	247.8	3.4	0.07	7	37.3
$\phi_{ra}p_{sr}$	248.6	4.2	0.04	8	36.0
$\phi_{sr}p_{sr}$	248.8	4.4	0.04	8	36.2
$\phi_{sra}p_{sr}$	251.5	7.1	0.01	10	34.6
$\phi_{sra}p_{s}$	252.4	8.0	0.00	8	39.8
$\phi_{sra}p_{sra}$	254.5	10.1	0.00	12	33.1
$\phi_{sra}p_{sa}$	254.5	10.1	0.00	9	39.8
$\phi_{sra}p_{r}$	256.6	12.2	0.00	8	44.0
$\phi_{sra}p_{ar}$	257.7	13.3	0.00	10	40.8
$\phi_{sra}p_{.}$	261.5	17.1	0.00	7	51.0
$\phi_{sra}p_{a}$	261.7	17.3	0.00	8	49.1
Ovenbird					
$\phi_{s}p_{r}$	457.2	0.0	0.77	4	23.9
$\phi_{sr}p_{r}$	461.0	3.8	0.12	6	23.5
$\phi_{sr}p_{.}$	462.8	5.5	0.05	5	27.4
$\phi_{sr}p_{sr}$	464.1	6.8	0.03	8	22.4
$\phi_{sr}p_{s}$	464.5	7.3	0.02	6	27.1
$\phi_{.}p_{r}$	465.2	7.9	0.01	3	33.9
$\phi_{r}p_{r}$	466.7	9.4	0.00	4	33.4

birds and between the sexes ($\phi_{.}p_{sr}$; Table 2). Overall, annual survival of American Redstarts was 0.55 ± 0.09 SE. The recapture rate was lowest for transient American Redstart females (0.09 ± 0.05 SE), followed by transient males (0.16 ± 0.06 SE), resident females (0.34 ± 0.14 SE), and resident males (0.90 ± 0.10 SE). This model (ϕp_{sr}) was 1.9 times more likely than the model that included sex specific differences in annual survival ($\phi_{s}p_{sr}$) and 2.2 times more likely than the model that included survival differences among resident and transient individuals ($\phi_{r}p_{sr}$; Table 2). Assuming sex specific differences in survival ($\phi_{s}p_{sr}$), our parameter estimates for female survival (0.72 ± 0.23 SE) were higher than that of males (0.52 ± 0.08 SE). Two females initially captured in 1993 that were not recaptured again until 1996 drove these results. When we removed these females from our analysis, female survival dropped to 0.39 ± 0.16 SE. However, the model selected as having the best fit was the same regardless of whether these two females were included in the data set or not. SY and ASY American Redstart males had identical survival values based on the model $\phi_{sa}p_{sr}$ (0.52 ± 0.15 SE and 0.52 ± 0.08 SE, respectively). The model providing the best fit to the Ovenbird data included sex specific differences in survival and differences in the recapture rate of resident and transient individuals ($\phi_{s}p_{r}$; Table 2). Annual survival of male Ovenbirds was 0.60 ± 0.05 SE and that of female Ovenbirds was 0.21 ± 0.09 SE. The recapture rate of resident birds was 0.62 ± 0.07 SE, which was much higher than for transient individuals (0.19 ± 0.06 SE). The model $\phi_{s}p_{r}$ was 6.4 times more likely than the model that incorporated the residency index in the estimation of survival rate ($\phi_{sr}p_{r}$).

Comparisons among studies.—We found 28 papers that reported return rates and/or survival estimates for Ovenbirds and American Redstarts (Table 3). Return rates of Ovenbirds ranged from 0.02–0.54, while return rates of American Redstarts ranged from 0.03–0.75. Few survival estimates based on robust methods such as Cormack-Jolly-Seber models were available with a range from 0.21–0.60 for Ovenbirds and 0.55–0.67 for American Redstarts. We detected no significant difference in the adjusted means for survival-return rate between Ovenbird (0.31) and American Redstarts (0.41; $\chi^2 = 3.2$, df = 1, $P = 0.076$). Robust estimates such as those provided by CJS models resulted in adjusted mean estimates of "survival" that were higher than those derived by simple return rate (0.61 and 0.28, respectively; $\chi^2 = 27.0$, df = 1, $P < 0.001$). Color banding also resulted in significantly higher estimates of "survival" than constant effort netting (0.48 and 0.27, respectively; $\chi^2 = 9.7$, df = 1, $P = 0.002$). Once we controlled for the other variables in the model, we could not detect any significant differences among the combined age-sex class (0.47), SY males (0.44), ASY males (0.49), AHY females (0.40), and AHY males (0.33; $\chi^2 = 2.6$, df = 4, $P = 0.63$).

DISCUSSION

To derive accurate estimates of survival required that we differentiate resident from transient individuals because transient individuals had a much lower probability of being recaptured than resident individuals. Resident individuals captured with constant effort netting, particularly males, had high recapture probabilities, suggesting that these individuals were returning to the same territory used during previous years. Similar results have been observed for Wilson's Warblers (*Wilsonia pusilla*), Song Sparrows (*Melospiza melodia*), Sedge Warblers (*Acrocephalus schoenobaenus*), and Winter Wrens (*Troglodytes troglodytes*; Chase et al. 1997). Although our residency index was crude, it was a more effective means of addressing violations of the assumption of homogeneity of capture than structuring the model to account for differential survival between the year after marking and subsequent periods. For both species, the two-stage model fit the data poorly, while combining the two-stage model with the residency index did not result in much improvement relative to the model with the residency index.

Previous studies have shown that unpaired territorial males and nonterritorial floaters are common in many Ovenbird and American Redstart populations (Sherry and Holmes 1989, Villard et al. 1993, Van Horn et al. 1995, Ortega and Capen 1999, Bayne and Hobson 2001). These results suggest that Ovenbird and American Redstart populations are male biased, possibly because survival of females is lower than that of males. Our data support this suggestion for Ovenbirds, as females had lower survival than that of males. Although this may reflect a true difference in survival between the sexes, our survival estimate for female Ovenbirds was unrealistically low and had a large error term associated with it. The extremely low survival rate of female Ovenbirds suggests that they had low site fidelity and were permanently dispersing from our sites. Alternatively, female Ovenbirds may have been more difficult to recapture than males, possibly because they were spending more time on the ground and moving around less.

In contrast to Ovenbirds, we detected no significant difference in survival of male and female American Redstarts, but we did detect a large difference in recapture rate. In fact, our estimates of survival for female American Redstarts were higher than those for males. The markedly different parameter estimates derived for female American Redstarts, depending on the inclusion of two birds, highlights the need to search for outliers when using CJS models. Regardless, these results suggest that female redstarts have lower territory fidelity than males. By moving just a few territories between years, female redstarts may greatly reduce the likelihood they will be recaptured. In contrast, resident male redstarts had an extremely high recapture rate, suggesting that they were returning to the same territory they used during previous years. Lemon et al. (1996) found that 59% ($n = 22$) of returning female and 76% ($n = 71$) of returning male American Redstarts returned to the same or adjacent territory. While we do not refute the premise that female survival is lower than that of males in passerine species (Greenwood and Harvey 1982), our results and the results of our literature review indicate that detecting such patterns can be difficult given the wide variety of other factors that influence estimates of survival.

Survival estimates for Ovenbirds and American Redstarts in the boreal forest were similar to those observed in other areas of their range. However, our estimates of survival, like all such estimates made on the breeding grounds, should be treated as minimum estimators of true survival. Our work in Saskatchewan (Bayne and Hobson 2002) and that of Porneluzi and Faaborg (1999) in Missouri, indicates male Ovenbirds that do not breed successfully are less likely to return to the same breeding territory in subsequent years than males that raise young. When Porneluzi and Faaborg (1999) excluded those individuals that did not raise young, their survival estimate for male Ovenbirds increased by 9%. If failed breeders captured on the breeding grounds are more likely to disperse in subsequent years, survival may be underestimated. This also appeared to be the case in one year for ASY American Redstart males investigated by Lemon et al. (1996). Given that previous breeding success may be a strong determinant of breeding site fidelity in warblers,

TABLE 3. Annual survival or return rate estimates (± SE) for adult Ovenbirds and American Redstarts from different studies conducted across the range of each species.

Study	Location	Sex[a]	*N*[b]	Years[c]	Survival-return rate	Method[d]
Ovenbird						
Hann 1948	Michigan	MF	38	10	0.54 ± 0.06	CB-R
Loftin et al. 1966	Panama	MF	143	2	0.02	CE-R
Anderson and Maxfield 1967	Massachusetts	MF	207	7	0.09	CE-R
Roberts 1971	Massachusetts	MF	27[e]	6	0.85 ± 0.07	CE-S[e]
Diamond and Smith 1973	Jamaica	MF	118	5	0.08	CE-R
Savidge and Davis 1974	Pennsylvania	MF	38[e]	6	0.54	CE-S[e]
Ely et al. 1977	Mexico	MF	79	7	0.16	CE-R
Rogers et al. 1982	Guatemala	MF	16	2	0.19	CE-R
Wander 1985	New Jersey	M,F	14/5	3	0.39/0.17	CB-R
Kricher and Davis 1986	Belize	MF	22	2	0.09	CE-R
Blake and Loiselle 1992	Costa Rica	MF	61	4	0.21	CE-R
Gonzalez-Alonso et al. 1992	Cuba	MF	26	2	0.19	CE-R
Conway et al. 1995	Belize	MF	312	2	0.24	CE-S
Faaborg and Arendt 1996	Puerto Rico	MF	28	17	0.43 ± 0.13	CE-S
Porneluzi and Faaborg 1999	Mississippi	M	74	4	0.52 ± 0.07	CB-S
Burke and Nol 2001	Ontario	M	74	4	0.36	CB-R
Murphy et al. 2001	San Salvador	MF	22	4	0.05	CE-R
DeSante et al. 2001	US Midwest	MF	368	5	0.49 ± 0.07	CE-S
This study	Saskatchewan	M	197	4	0.60 ± 0.06	CECB-S
This study	Saskatchewan	F	76	4	0.21 ± 0.09	CE-S
American Redstart						
Anderson and Maxfield 1967	Massachusetts	MF	44	7	0.03	CE-R
Diamond and Smith 1973	Jamaica	MF	126	5	0.12	CE-R
Nichols et al. 1981	New Hampshire	MF	—	11	0.67	CB-S
McNeil 1982	Venezuela	MF	9	2	0.44	CE-R
Rogers et al. 1982	Guatemala	MF	13	2	0.15	CE-R
Holmes and Sherry 1992	Jamaica	M	69/42	4	0.75, 0.49[f]	CB-R
Holmes and Sherry 1992	Jamaica	M	69/42	4	0.46	CB-R
Holmes and Sherry 1992	New Hampshire	M	83/51	6	0.16, 0.39[f]	CB-R
Holmes and Sherry 1992	New Hampshire	F	48	6	0.19	CB-R
Lemon et al. 1996	New Brunswick	M	~300	~10	0.26, 0.44[f]	CB-R
Lemon et al. 1996	New Brunswick	F	112	~10	0.21	CB-R
Wunderle and Latta 2000	Dominican Rep.	M	48/27	3	0.30, 0.41[f]	CB-R
Wunderle and Latta 2000	Dominican Rep.	F	52	3	0.39	CB-R
Marra and Holmes 2001	Jamaica	M	86/106	5	0.61, 0.70	CB-R
Marra and Holmes 2001	Jamaica	F	78	5	0.62	CB-R
Marra and Holmes 2001	Jamaica	M	25/10	5	0.44, 0.40[f]	CB-R
Marra and Holmes 2001	Jamaica	F	63	5	0.37	CB-R
Murphy et al. 2001	San Salvador	MF	21	4	0.24	CE-R
This study	Saskatchewan	MF	212	4	0.55 ± 0.09	CE-S

[a] Composition of sample at time of marking in respect to sex. MF = combined males and females in estimate. M,F = male and female survival calculated separately.
[b] Number of individuals released.
[c] Number of years sampled.
[d] Method used to capture birds and generate survival/return rate estimate (CB = color banding, CE = constant effort netting, r = return rate, S = survival corrected for recapture rate).
[e] Survival estimates based on correcting return rate for presence of transients.
[f] SY and ASY males, respectively.

and assuming it has little influence on winter site fidelity, the most accurate assessments of survival may be obtained on the wintering grounds (Holmes and Sherry 1992, Sandercock and Jamerilo 2002). However, considerable variation also exists in return rates to wintering areas (Murphy et al. 2001) suggesting that individual variation also may have a strong influence on fidelity to nonbreeding sites. Nevertheless, adult survival estimates

that are more easily obtained from breeding ground data would benefit from more long term banding studies using CJS models rather than simple return rates to estimate survival.

We were unable to detect a significant difference in survival of male Ovenbirds generated by constant effort and playback netting. However, our estimate from the pooled data was higher than when we used only constant effort netting to assess survival. While our inference regarding the importance of capture method is weak due to the fact that our comparison of methods is confounded by temporal and spatial variation in survival (Sillett et al. 2002), it suggests that playback netting may be a more effective way of establishing survival and return rates (but see Nur et al. 1999). This assertion is supported by our review of other studies that show a much higher return rate-survival estimate when color banding is used relative to constant effort netting. However, most of the constant effort netting examined in our review did not separate transients from residents. The intensive effort required by playback netting may make it a less useful alternative to assess passerine survival than constant effort schemes. Where it is desirable to capture females, constant effort netting also may be the only viable method to capture large numbers of individuals. A compromise that we suggest is to color band captured individuals and spot map a fixed area surrounding the net lane, which might provide a more accurate assessment of which individuals were residents, and thus improve the accuracy of survival estimates generated from constant effort netting.

This study is one of the first to report survival rates of American Redstarts and Ovenbirds at the northern edge of their range. Our results are similar to or higher than those generated in more southern locations, suggesting that site fidelity and survival of American Redstarts and Ovenbirds in boreal environments is similar to other biomes. However, more work on survival rates of boreal passerines is required, particularly as it relates to habitat and landscape change (Bayne and Hobson 2002). Our results illustrate the importance of identifying transient individuals when estimating recapture rates. In addition to identifying transients, future work should endeavor to identify individual and possibly habitat specific characteristics that influence survival and recapture rate (i.e., breeding success). Regardless, the residency index used here seems to provide a more effective means of identifying transients than two-stage models and should be incorporated in models that attempt to estimate passerine survival.

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A CROSS-CANADA COMPARISON OF MASS CHANGE IN BIRDS DURING MIGRATION STOPOVER

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ABSTRACT.—I estimated hourly mass change at stopover sites for 14 species of migrant passerines from 15 sites across southern Canada by analyzing size-corrected mass of birds at first capture as a function of time of day of handling. Mean mass gains were 0.40% of lean body mass/h during spring and 0.53% during fall. Mass gain estimates varied significantly with season, site, and species, and were negatively related to condition of birds in the early morning. However, standard errors were large, such that few individual estimates were significantly different. Several sites with consistently low rates of mass gain had characteristics that probably reduced local food supply. Swainson's Thrushes (*Catharus ustulatus*) also had consistently low rates of mass gain. I estimated the time required to accumulate sufficient mass to fuel a 10-h migratory flight, and found that the majority of estimated mass gains were sufficient for birds to refuel during <1 week of stopover in southern Canada. At mean rates of mass gain from this study, migrants in southern Canada could potentially refuel completely during 2–3 days in both seasons, but true periods are likely somewhat longer. Analysis of mass change along migration routes (instead of across them, as in this study) is needed to detect whether there are differences among species in timing and location of maximum fuel deposition, as has been found in Europe.
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Between migratory flights, birds must replenish energy stores in order to successfully complete their journeys, and the rate at which birds change mass during stopover should be an index of site quality. This measure reflects food abundance as well as incorporating effects of weather conditions, levels of competition and predator harassment, and other external factors that could affect mass change. However, endogenous factors also affect fattening rates, and must be taken into account when interpreting mass change with respect to site quality. For example, birds with optimal fat stores should maintain mass rather than gain more, and optimal fuel loads may vary according to proximity to the final destination or to large geographic barriers such as the Gulf of Mexico. Finally, there may be differences in migratory strategy among species, such as speed of migration or length of migratory flights, that also could affect mass change patterns.

Study of mass change at many sites across a large geographic area may help to tease these factors apart. The only example of such a study to date on nocturnally migrating passerines involved six species captured at 34 sites distributed from northern Europe to North Africa (Schaub and Jenni 2000). Results showed marked differences among species in overall migration strategy, with variation in the time period and location at which maximum fuel loads were accumulated. Such differences have important implications for conservation planning and protection of stopover sites. Similar variation is likely in North American passerine migrants, yet there are only a few studies that have compared mass change among sites, and these were very limited in geographic scope (Dunn 2000, 2001).

Here I compare mass change of 14 species of nocturnally migrating passerines at 15 sites across southern Canada, with the aim of detecting and explaining variation in mass gain among locations. Sample sites were distributed across the main migration routes (Brewer et al. 2000) rather than along a path between breeding and wintering areas. Because all sites were close to the breeding grounds of the target species and distant from major geographic barriers, I expected variation in physiological condition and migratory motivation to be small. Any marked and consistent variation in mass change, therefore, likely would be related to the quality of sites and their surrounding landscapes. The second aim of the study was to estimate the amount of time it would take for actively migrating birds to refuel in southern Canada following depletion of fat reserves. While many assumptions were involved in the model, it provided context for interpretation of the mass change estimates.

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FIG. 1. The Canadian Migration Monitoring Network stations contributing data on mass change during migration stopover to this study were distributed across all of southern Canada. Station names are shown in Table 1.

METHODS

I assessed mass change by regression of mass at first capture on time of day (Morris et al. 1996, Jones et al. 2002). Assumptions of this method are discussed in Winker et al. (1992), Winker (1995), and Dunn (2000, 2001).

Data set.—Data from 15 sites were contributed by 13 member stations in the Canadian Migration Monitoring Network (CMMN), including the three stations operated by Long Point Bird Observatory (LPBO; Fig. 1). I chose 14 target species for analysis (see results) because they were broadly distributed across Canada and large numbers were captured at many CMMN stations. All were small nocturnal migrants, ranging in mean mass from 6.6–31.5 g (median = 12.0 g).

All birds included in analyses were caught in mist nets or in Heligoland traps (Hussell and Woodford 1961). Birds caught in baited ground traps were excluded due to the likelihood of unusual mass gain due to eating baits. Nets were opened at or before dawn and were run for ≥6 h on a daily basis during one or both migration seasons, weather permitting. Birds were transported and held individually in cloth bags or holding boxes until banding, at which time wing chord was measured (unflattened, to the nearest mm) and birds were weighed (usually to the nearest 0.1 g on a triple beam balance or electronic scale). Fat in furcular deposits was scored using a variety of scoring systems, but in all cases it was possible to identify birds that had no fat or only a trace amount of fat, and these were the only fat data used in this paper. Time of day was recorded as shown in Table 1, usually to the nearest 10 min. For this analysis, I expressed times as decimal values and converted them to h after local sunrise to account for progressive change in timing of sunrise during each season. For each site, I applied the sunrise data for 1999 to all years, since variance in the time of sunrise among years was trivial.

Most data came from the late 1990s, but LPBO data covered the 1980s as well. Unless there are long term trends in conditions affecting mass change at a particular site, comparisons among sites should not be affected by variation in the time periods analyzed. Dunn (2000) demonstrated annual variation in rate of mass change and recommended that estimates be based on several years of data to best reflect typical conditions, but those results gave no evidence of long term trends.

To standardize hours of coverage among sites, I limited analysis for each species to data from the first 7 h after sunrise. A few sites operated for only 6 h, but birds captured at the end of the day often were weighed after nets were closed, and the 7-h cutoff al-

TABLE 1. Mass change data of migrating passerines were obtained from 15 stopover sites.

Station	Seasons[a]	Years in sample	Time recorded[b]
Atlantic Bird Observatory (Bon Portage), NS (ABO)	F	1996–98	CS
Beaverhill Bird Observatory, AB (BBO)	B	1997–98	CE
Delta Marsh Bird Observatory, AB (DMBO)	S	1992–99	W (1992–94), CS
Delta Marsh Bird Observatory, AB (DMBO)	F	1995–99	CS
Innis Point Bird Observatory, ON (IPBO)	F	1997–99	W
Inglewood Bird Sanctuary, AB (IBS)	B	1995–99	CS
Haldimand Bird Observatory (Selkirk), ON (HBO)	S	1996–99	CE
Last Mountain Bird Observatory, SK (LMBO)	B	1989–99	W
Lesser Slave Lake Bird Observatory, AB (LSLBO)	B	1994–99	C
Long Point Bird Observatory, ON (LPBO): 3 sites	B	1980–96	CM+W
Mackenzie Nature Observatory, BC (MNO)	F	1996–99	CS
Prince Edward Point Bird Observatory, ON (PEPtBO)	S	1995–99	W
Rocky Point Bird Observatory, BC (RPBO)	F	1999	CS
Thunder Cape Bird Observatory, ON (TCBO)	B	1991–98	CM+W

[a] Season for which data were contributed. S = spring, F = fall, B = both.

[b] C = time of capture. CS = start of net check, CM = approximate middle of net check, CE = end of net check, W = time of weighting. Where both capture and time of weighing were recorded (CM+W), time of capture was used in analyses.

lowed these individuals to be included. For each site, I deleted records of individuals with mass or wing length falling below the 1st percentile or above the 99th percentile of all measurements taken at that site, to exclude possible errors in measurement or recording. I also restricted the data for each species from a given site to the species specific migration period at that site. This was determined by plotting number of birds weighed against date and, for species that summer or winter at or near that site, eliminating data beyond the range of dates during which there was a marked build-up to, and drop-off from, a strong seasonal peak in numbers banded. This limitation, and the fact that I included only first captures in the analyses, minimized the inclusion of locally breeding or overwintering individuals. I did not analyze data for a species unless the final data set for the site and season included ≥100 individuals.

Statistical analyses.—I adjusted mass for body size by calculating a condition index (CI = mass × 100/wing length, in which multiplication by 100 reduces rounding error). Some previous analyses used a different index (e.g., mass × 10,000/wing length^3; Winker et al. 1992, Dunn 2001). However, Winker (1995) found that the newer formula was more effective at correcting mass for structural body size. The regression model was $CI = b_0 + b_1H$, where H is the time of day of capture or weighing, expressed as h after sunrise. The coefficient b_1 is the estimate of hourly change in condition index and can be converted to hourly change in mass using the formula: mass change $= b_1$(wing length)/100. Wing length used in the conversion was the mean for each species, specific to site and season. The result gave an estimate of hourly mass change for a bird of mean wing length at mean date of capture for the site and season.

The sites contributing to this study recorded time of day of handling in different ways (Table 1). I analyzed data for 39 species from three high volume sites where times were recorded for both capture and weighing, and found that when the latter was used in analysis instead of time of capture, mass change estimates were slightly reduced (due to mass loss prior to weighing; Dunn 1999). However, the mean reduction was only 2% (EHD unpubl. data), so any effect of variation in weighing time among contributing sites should be small.

I compared mass change over the first 7 h after sunrise to mass change over the same period exclusive of the first hour, to determine whether there was an initial rapid gain due to birds filling their guts after a night of fasting. The mean 7-h mass change was only slightly higher than the 6-h change (0.015% of lean mass/h, paired $t_{123} = 1.09$, $P = 0.18$), but there was no consistent pattern among cases in whether the mass change estimate increased or decreased when birds captured during the first hour were omitted. Results presented here are for the full 7-h period, to take advantage of the larger sample size. Two sites, LPBO and Thunder Cape Bird Observatory regularly operated for ≥12 h. For these sites, I estimated mass change over the first 12 h after sunrise, as well as over the first 7 h, to investigate variation in rate of mass change over the course of the day.

I converted all estimates of hourly mass change to percent of lean body mass to allow direct comparison among species of different body size. I defined lean body mass for each species (calculated separately for each site and season to account for any differences in populations being sampled) as the mean mass for birds classified as having no visible fat in the furculum. In a few cases, the mean mass for birds with no fat and a trace of fat combined was lower than the mean for birds with no fat alone (apparently due to individual variation in fat scoring), in which case the lower value was taken as the lean mass. Readers should note that

this definition of lean differs from the conventional definition, usually meaning fat free.

For an index of mean physiological condition of birds at a site during early morning, I calculated mean mass during the first 3 h after sunrise, subtracted lean mass (mass of birds with no visible fat) and expressed the difference as a percent of lean mass to remove effects of different body size among species; small samples at some sites precluded use of data from the first hour or two alone. I examined variation in morning condition according to site, season, and species using general linear models (GLM). I also used GLM to examine the effect of these factors and of morning condition on hourly mass gain, using Tukey's studentized range test to evaluate the significance of effects.

Estimates of hourly mass change can be interpreted more easily if compared with some threshold value, which was defined here as the energetic break even point over 24 h during which no migration takes place. For each species, I estimated overnight energy use as existence energy costs (Kendeigh 1970) between sunset and sunrise at the mean passage date for the site and season. I then converted energy use to mass loss, on the assumption that all energy came from burning fat (see Dunn 2001 for additional details and justification of assumptions). This threshold value must be surpassed with energy gain during daytime feeding if energy is to be accumulated for fueling of continued migration. While based on many assumptions, this value can be used as a general reference point for interpreting results of mass change analyses.

For each site, season, and species, I estimated the number of days of refueling that would be required for a lean bird (one without visible fat) to gain enough mass to sustain a 10-h migratory flight without falling below its lean mass. I conducted two analyses: one assuming that rate of change over the first 7 h of the day would be continued over all daylight hours (specific to season, site, and species), and the other assuming no further gain or loss during daylight hours subsequent to 7 h of feeding. For these estimations I assumed that mass loss on nights without migration was the threshold value described above, and that hourly mass loss during migration was $0.0533 \times \text{mass}^{0.40}$ (Hussell and Lambert 1980). The latter formula was based on mass loss experienced by nine small passerine species during actual nocturnal migration (exclusive of Blackpoll Warbler, *Dendroica striata*, for which mass loss was exceptionally low), and amounted to about 0.9% of body mass/h.

Mass change estimates are presented as the estimate ± SE, expressed as percent of lean body mass/h. Results were considered significant if $P < 0.05$. Other mean values are shown as the estimate ± SD.

RESULTS

Hourly mass change estimates for each site and season are listed in Table 2. Mean rates were 0.40% of lean body mass/h during spring ($n = 76$) and 0.53% during fall ($n = 106$). Comparison of values for species-sites for which results were available from both seasons showed that fall values were significantly higher (paired $t_{52} = 2.18$, $P = 0.034$), and were less likely to fall below threshold values (19% of cases during fall versus 38% during spring).

Standard errors of mass change estimates were high, so there were few significant differences among estimates (Table 2), despite their spanning a broad range of values (−0.66 to 1.95% of lean mass/h). Nonetheless, there were some exceptions. During spring there were three sites at which fewer than half of the species met or surpassed threshold values (Beaverhill and Last Mountain bird observatories, and site 1 at LPBO; Table 3). During fall, only Atlantic Bird Observatory had a low proportion of species surpassing their thresholds. Delta Marsh Bird Observatory had a particularly high mean mass change during spring, as did Rocky Point Bird Observatory during fall (Table 3).

Table 4 shows a similar summary of data for species. During spring, there were two species that failed to attain or surpass threshold mass change at half or more of the sites for which they were analyzed: Swainson's Thrush (*Catharus ustulatus*), and White-crowned Sparrow (*Zonotrichia leucophrys*). During fall, only the Swainson's Thrush fell below this level.

The mean value of early morning mass (first 3 h after sunrise) relative to lean mass was low (1.20 ± 2.87% above lean body mass, $n = 182$). However, this index of early morning condition varied significantly with species, site, and season (Table 5). For species-sites for which there were data for both seasons, early morning mass was higher during spring than during fall (1.21% versus −0.05% above lean mass, respectively; paired $t_{52} = 3.74$, $P < 0.001$). Among species, Swainson's Thrushes were the heaviest during early morning (5% above lean mass during spring and 2.8% above during fall). Among sites, early morning mass was highest at Delta Marsh and Haldimand bird observatories during spring (5.4% and 8.7% above lean mass, respectively), and at Atlantic Bird Observatory during fall (6.3% above lean mass). Rate of mass gain was negatively related to the difference between early morning and lean mass

TABLE 2. Estimated rates of mass change[a] during migration stopover covered a wide range of values, but had large standard errors. Most estimates showed mass gain sufficient to support a 10-h migratory flight within 1 week (median = 4 days during spring and 3 days during fall). See Table 1 for site names.

Species and site	Spring				Difference between seasons	Fall			
	n	Difference[b]	Mass change (mean ± SE)	Days to refuel[c]		*n*	Difference	Mass change (mean ± SE)	Days to refuel[c]
Least Flycatcher, *Empidonax minimus*									
BBO	117	a	−0.43 ± 0.33	—		198	b	0.43 ± 0.21	4
DMBO	226	a	0.61 ± 0.28	2		380	ab	0.67 ± 0.17	2
LMBO	292	a	0.12 ± 0.31	—	*	683	a	1.39 ± 0.25	1
LPBO-1	1,415	a	0.07 ± 0.09	—	*	1,612	b	0.66 ± 0.09	2
LPBO-2	424	a	0.21 ± 0.20	—		571	b	0.52 ± 0.15	3
LPBO-3	653	a	0.40 ± 0.15	4		618	b	0.45 ± 0.16	4
LSLBO	330	a	0.22 ± 0.21	8		210	b	0.06 ± 0.23	—
MNO						324	b	0.40 ± 0.15	3
TCBO						143	b	0.21 ± 0.28	—
Ruby-crowned Kinglet, *Regulus calendula*									
DMBO						236	b	0.75 ± 0.18	3
HBO	411	a	0.89 ± 0.24	2					
IPBO						102	bc	0.44 ± 0.32	20
LMBO						251	abc	0.72 ± 0.23	4
LPBO-1	1,490	b	−0.23 ± 0.11	—		2,188	c	0.09 ± 0.09	—
LPBO-2	1,774	b	−0.25 ± 0.11	—					
LPBO-3	2,980	a	0.48 ± 0.08	5		5,135	b	0.72 ± 0.06	4
MNO						898	b	0.56 ± 0.10	4
PEPtBO	1,013	a	0.85 ± 0.17	2					
RPBO						181	a	1.73 ± 0.29	2
TCBO	106	ab	0.16 ± 0.45	—		374	ab	0.78 ± 0.19	4
Swainson's Thrush, *Catharus ustulatus*									
DMBO	122	a	0.69 ± 0.56	1		262	a	0.11 ± 0.34	—
HBO	169	a	0.06 ± 0.33	—					
IBS						102	a	−0.19 ± 0.46	—
LMBO	139	a	−0.20 ± 0.61	—		182	a	0.43 ± 0.40	2
LPBO-1	305	a	−0.60 ± 0.35	—		1,319	a	−0.10 ± 0.11	—
LPBO-2	216	a	−0.03 ± 0.36	—		1,036	a	−0.04 ± 0.12	—
LPBO-3	504	a	0.20 ± 0.22	5		1,707	a	0.10 ± 0.09	—
MNO						250	a	0.38 ± 0.22	2
PEPtBO	149	a	−0.57 ± 0.48	—					
TCBO						926	a	0.14 ± 0.12	—
Tennessee Warbler, *Vermivora peregrina*									
BBO						149	ab	0.23 ± 0.33	20
DMBO						1,345	b	0.09 ± 0.11	—
LMBO						440	a	1.21 ± 0.28	1
LPBO-1						235	ab	0.41 ± 0.29	6
LPBO-2						545	ab	0.67 ± 0.23	3
LPBO-3	307	b	−0.21 ± 0.38	—		358	a	0.93 ± 0.22	2
TCBO	515	a	1.17 ± 0.18	1	*	841	ab	0.45 ± 0.15	4
Magnolia Warbler, *Dendroica magnolia*									
HBO	229	a	0.81 ± 0.32	2					
LMBO						223	a	0.78 ± 0.29	2
LPBO-1	600	b	−0.66 ± 0.20	—	*	723	a	0.93 ± 0.15	2
LPBO-2	509	ab	0.22 ± 0.24	—		1,649	a	0.58 ± 0.10	4
LPBO-3	2,890	a	0.02 ± 0.09	—	*	1,732	a	0.65 ± 0.10	3
LSLBO						101	a	0.16 ± 0.37	—
MNO						200	a	0.44 ± 0.20	4
PEPtBO	485	a	0.23 ± 0.23	25					
TCBO	330	a	0.39 ± 0.19	4		659	a	0.45 ± 0.14	5

TABLE 2. Continued.

Species and site	Spring				Difference between seasons	Fall			
	n	Difference[b]	Mass change (mean ± SE)	Days to refuel[c]		*n*	Difference	Mass change (mean ± SE)	Days to refuel[c]
Yellow-rumped Warbler, *D. coronata*									
ABO						512	abc	0.26 ± 0.22	—
BBO						429	abc	0.36 ± 0.16	6
DMBO	279	a	1.03 ± 0.35	1		580	ab	0.57 ± 0.14	3
HBO	258	ab	0.25 ± 0.28	11					
IBS						1,084	ab	0.68 ± 0.13	2
IPBO	446	a	0.43 ± 0.24	3					
LMBO	260	ab	0.05 ± 0.36	—		4,025	c	0.26 ± 0.06	—
LPBO-1	900	b	−0.43 ± 0.15	—	*	3,135	c	0.16 ± 0.07	—
LPBO-2	595	ab	−0.04 ± 0.20	—		207	abc	0.67 ± 0.24	3
LPBO-3	614	a	0.63 ± 0.19	2		5,155	a	0.66 ± 0.06	3
LSLBO	172	ab	0.24 ± 0.27	7		673	bc	0.32 ± 0.11	7
MNO						328	bc	0.14 ± 0.16	—
PEPtBO	813	a	0.35 ± 0.16	4					
TCBO	323	a	0.31 ± 0.21	5		675	abc	0.37 ± 0.14	12
Blackpoll Warbler, *D. striata*									
ABO						218	a	−0.06 ± 0.46	—
LMBO						623	a	0.39 ± 0.17	5
LPBO-1						1,333	a	0.73 ± 0.11	2
LPBO-2						708	a	0.60 ± 0.16	3
LPBO-3	104		1.95 ± 0.51	1		388	a	0.75 ± 0.20	2
TCBO						348	a	0.25 ± 0.21	—
American Redstart, *Setophaga ruticilla*									
ABO						149	b	−0.14 ± 0.39	—
DMBO	153	a	1.64 ± 0.42	1		408	ab	0.93 ± 0.17	2
LMBO						456	ab	0.56 ± 0.18	3
LPBO-1	213	c	−0.04 ± 0.31	—		498	ab	0.47 ± 0.16	6
LPBO-2	154	ab	1.36 ± 0.30	1	*	637	b	0.37 ± 0.15	11
LPBO-3	515	bc	0.43 ± 0.18	4		831	ab	0.72 ± 0.13	3
LSLBO	423	c	0.28 ± 0.18	6		831	ab	0.52 ± 0.12	3
MNO						1,150	ab	0.69 ± 0.09	2
PEPtBO	206	a	0.63 ± 0.29	2					
TCBO	460	c	0.36 ± 0.15	5	*	1,553	a	0.90 ± 0.10	2
Northern Waterthrush, *Seiurus noveborecensis*									
ABO						131	a	0.57 ± 0.27	2
DMBO						365	a	0.79 ± 0.21	1
IBS						180	a	0.79 ± 0.29	1
LMBO						215	a	0.19 ± 0.34	36
LPBO-1						262	a	0.95 ± 0.29	1
LPBO-2	140	a	0.42 ± 0.38	3		822	a	0.20 ± 0.16	—
LPBO-3	132	a	0.74 ± 0.45	1		313	a	0.60 ± 0.26	2
MNO						887	a	0.31 ± 0.10	4
TCBO						376	a	0.40 ± 0.22	3
Wilson's Warbler, *Wilsonia pusilla*									
DMBO	171	a	1.78 ± 0.50	1					
IBS						516	a	0.84 ± 0.18	2
LMBO						482	a	0.37 ± 0.27	7
LPBO-1	136	b	−0.21 ± 0.44	—		233	a	0.94 ± 0.28	2
LPBO-2	190	ab	0.68 ± 0.37	2		240	a	0.84 ± 0.27	2
LPBO-3	617	ab	0.47 ± 0.21	4		388	a	0.99 ± 0.23	2
LSLBO						120	a	0.96 ± 0.37	2
MNO						309	a	0.86 ± 0.15	2
RPBO						236	a	0.55 ± 0.16	3

TABLE 2. Continued.

Species and site	Spring				Difference between seasons	Fall			
	n	Difference[b]	Mass change (mean ± SE)	Days to refuel[c]		*n*	Difference	Mass change (mean ± SE)	Days to refuel[c]
Lincoln's Sparrow, *Melospiza lincolnii*									
IBS						154	a	1.13 ± 0.39	1
LMBO						232	a	0.50 ± 0.31	3
LPBO-1	651	a	0.16 ± 0.18	—					
LPBO-2	407	a	0.83 ± 0.27	1					
LPBO-3	551	a	0.38 ± 0.20	3					
MNO						117	a	0.31 ± 0.45	4
PEPtBO	105	a	0.13 ± 0.43	—					
RPBO						138	a	0.98 ± 0.36	1
TCBO						188	a	1.06 ± 0.25	1
White-throated Sparrow, *Zonotrichia albicollis*									
ABO						114	ab	0.07 ± 0.46	—
DMBO	270	a	1.72 ± 0.25	1		399	a	1.04 ± 0.19	1
HBO	559	b	0.49 ± 0.18	2					
IBS						210	ab	0.38 ± 0.32	3
IPBO	110	ab	0.87 ± 0.38	1					
LMBO	223	bc	0.36 ± 0.31	2		412	ab	0.43 ± 0.21	3
LPBO-1	4,333	c	−0.05 ± 0.06	—		1,056	b	0.17 ± 0.11	—
LPBO-2	3,040	b	0.56 ± 0.07	1					
LPBO-3	3,767	b	0.57 ± 0.06	1		2,123	a	0.71 ± 0.09	1
LSLBO	262	abc	0.67 ± 0.30	1		162	ab	0.52 ± 0.24	2
PEPtBO	719	ab	0.91 ± 0.18	1					
TCBO	204	ab	0.65 ± 0.29	1		236	ab	0.34 ± 0.21	3
White-crowned Sparrow, *Z. leucophrys*									
LPBO-1	1,072	b	0.02 ± 0.15	—		467	a	0.20 ± 0.19	—
LPBO-2	1,051	b	0.00 ± 0.15	—					
LPBO-3	119	a	1.38 ± 0.46	1		204	a	0.64 ± 0.30	2
MNO						108	a	0.39 ± 0.29	2
TCBO						237	a	0.95 ± 0.22	1
Dark-eyed Junco, *Junco hyemalis*									
DMBO						274	ab	0.70 ± 0.18	2
HBO	253	ab	0.39 ± 0.27	3					
IPBO	192	a	0.77 ± 0.24	1		119	ab	0.52 ± 0.36	3
LMBO						1,082	ab	0.53 ± 0.12	3
LPBO-1	2,154	b	−0.15 ± 0.09	—		1,766	b	0.27 ± 0.09	—
LPBO-2	1,016	a	0.44 ± 0.12	3					
LPBO-3	784	a	0.43 ± 0.15	3		930	a	0.84 ± 0.12	2
MNO						435	b	0.16 ± 0.15	—
PEPtBO	314	a	0.84 ± 0.25	1					
TCBO	482	ab	0.14 ± 0.16	—		2,421	a	0.61 ± 0.07	2

[a] Mass change ± SE, expressed as % of lean body mass/h.

[b] Within species and season, sites not sharing a letter in common were significantly different (Tukey's studentized range tests). Asterisks in the center column indicate significant differences in seasonal values.

[c] Calculation based on the assumption that hourly rate of mass gain was maintained over all daylight hours. A dash indicates that mass was being lost, or gained at a rate insufficient to support a full night of migration within 40 days.

(Table 5), such that a species with early morning mass 5% above lean mass would be expected to have an hourly rate of mass gain about 15% below that of a species starting the day at lean mass.

Estimates of the number of days required to build up enough fuel to sustain 10 h of migration without falling below lean mass (based on the assumption that estimated hourly mass change continued over all daylight h) showed that most birds could completely refuel in ≤1 week (59% of species during

TABLE 3. Sites varied in mean mass change values and in the percent of species achieving net gains over 24-h. Although sites differed in the suite of species analyzed, three sites (BBO, LMBO, and LPBO-1) had consistently low values during spring, and one (ABO) during fall. See Table 1 for site names.

	Spring				Fall			
Site	Mean mass change[a]	Mean threshold[b]	Percentage over threshold[c]	Number of species	Mean mass change	Mean threshold	Percentage over threshold	Number of species
ABO					0.14	0.27	20	5
BBO	−0.43	0.14	0	1	0.34	0.21	100	3
DMBO	1.25	0.14	100	6	0.63	0.22	78	9
HBO	0.48	0.19	83	6				
IBS					0.61	0.20	83	6
IPBO	0.69	0.17	100	3	0.48	0.33	100	2
LMBO	0.08	0.13	25	4	0.60	0.23	100	13
LPBO-1	−0.19	0.18	9	11	0.45	0.27	54	13
LPBO-2	0.37	0.18	67	12	0.49	0.26	89	9
LPBO-3	0.56	0.18	86	14	0.67	0.27	92	13
LSLBO	0.35	0.13	100	4	0.42	0.19	67	6
MNO					0.42	0.18	82	11
PEPtBO	0.42	0.18	75	8				
RPBO					1.09	0.30	100	3
TCBO	0.45	0.17	71	9	0.53	0.24	77	13

[a] Mean of species values, expressed as % of lean body mass/h.
[b] Mean across species of hourly mass gain that must be met or surpassed for mass equilibrium over 24 h with no migration (see Methods).
[c] Percentage of species with data from this site that met or surpassed their thresholds for 24-h mass balance.

spring and 73% during fall; Table 2). Median time to refuel was 4 days during spring and 3 days during fall. At the mean rates of mass change (0.40% of lean body mass/h during spring and 0.53% during fall), estimated refueling time for 12 and 20 g birds was 2–3 days, regardless of season (Fig. 2A). Larger birds required shorter refueling periods because maintenance costs decrease in proportion to increased mass. Refueling time was very sensitive to changes in mass gain up to about 1.75 times the gain needed to maintain

TABLE 4. Compared to other migrating passerines, the Swainson's Thrush stood out as having consistently low rates of mass change at most sites, during both seasons.

	Spring				Fall			
Species	Mean mass change[a]	Mean threshold[b]	Percent over threshold[c]	Number of sites	Mean mass change	Mean threshold	Percent over threshold	Number of sites
American Redstart, *Setophaga ruticilla*	0.67	0.18	86	7	0.56	0.24	89	9
Blackpoll Warbler, *Dendroica striata*	1.95	0.17	100	1	0.44	0.25	67	6
Least Flycatcher, *Empidonax minimus*	0.17	0.16	57	7	0.53	0.21	78	9
Lincoln's Sparrow, *Melospiza lincolnii*	0.38	0.16	75	4	0.80	0.21	100	5
Magnolia Warbler, *D. magnolia*	0.17	0.20	67	6	0.57	0.25	86	7
Yellow-rumped Warbler, *D. coronata*	0.28	0.18	70	10	0.40	0.27	73	11
Northern Waterthrush, *Seiurus noveboracensis*	0.58	0.16	100	2	0.53	0.18	100	9
Ruby-crowned Kinglet, *Regulus calendula*	0.32	0.25	50	6	0.72	0.38	88	8
Dark-eyed Junco, *Junco hyemalis*	0.41	0.18	71	7	0.52	0.26	71	7
Swainson's Thrush, *Catharus ustulatus*	−0.06	0.12	29	7	0.10	0.17	25	8
Tennessee Warbler, *Vermivora peregrina*	0.48	0.18	50	2	0.57	0.23	86	7
White-crowned Sparrow, *Zonotrichia leucophys*	0.47	0.13	33	3	0.55	0.21	75	4
Wilson's Warbler, *Wilsonia pusilla*	0.68	0.21	75	4	0.79	0.26	100	8
White-throated Sparrow, *Z. albicollis*	0.68	0.13	90	10	0.46	0.21	75	8

[a] Mean of site values, expressed as % of lean body mass/h.
[b] Mean across sites of hourly mass gain that must be met or surpassed for mass equilibrium over 24 h with no migration (see Methods).
[c] Percentage of sites at which species met or surpassed its threshold for 24-h mass balance.

TABLE 5. Morning condition (the difference between mean mass during the first 3 h of the day and lean mass, expressed as % of lean mass) varied with season, site and species (general linear models). Rate of mass gain also varied with these factors, and decreased with improved morning condition.

Source of variation	df	SS	*F*	*P*
Morning condition				
Season	1	88.49	30.42	<0.001
Species	13	207.67	5.49	<0.001
Site	14	747.01	18.34	<0.001
Rate of mass gain				
Season	1	0.74	6.20	0.01
Species	13	5.39	3.50	<0.001
Site	14	8.23	4.95	<0.001
Morning condition	1	1.17	14.05	<0.001

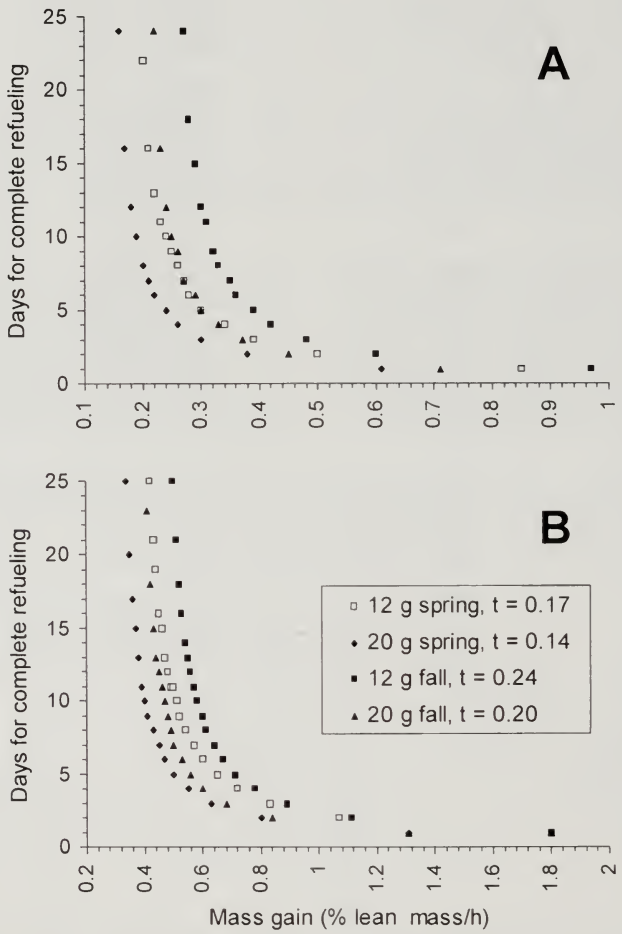

FIG. 2. Results of a model estimating days required for lean birds of two sizes to gain sufficient mass in southern Canada to undertake a 10-h migratory flight without falling below their lean mass (see Methods). (A) Birds were assumed to gain mass during every daylight hour (15 h during spring and 13 h during fall). (B) Birds gained mass for 7 h and maintained stable mass over the remaining daylight hours. Birds in Fig. 2A could fly for 10 h after 2–3 days of refueling in both seasons, whereas refueling time in Fig. 2B rose to as much as 3 weeks (note difference in x-axis scales).

24-h mass balance, after which increased rate of gain made relatively little difference.

When mass change was assumed to cease after 7 h (with mass maintained, but not increased over remaining daylight hours), refueling curves shifted to the right (Fig. 2B). Birds gaining for only 7 h would have to double their hourly mass gain in order to refuel as fast as birds that gained mass throughout the day.

At sites where data often were collected for ≥12 h (Thunder Cape Bird Observatory and LPBO), hourly mass change estimates based on 12 h were significantly higher than those based on 7 h during spring (0.46% of lean mass/h versus 0.31%, respectively; paired $t_{45} = 4.02$, $P < 0.001$), but were not significantly different during fall (0.57% of lean mass/h versus 0.53%, respectively; paired $t_{48} = 1.49$, $P = 0.14$). Results were similar for each season at each site.

DISCUSSION

Although estimates of hourly mass change varied widely, confidence intervals were so broad that there were few significant differences among them. Wide confidence intervals are inevitable in analyses of this kind because there will nearly always be large variation in individual mass at any given time of day. This variation results from factors such as length of stopover prior to first capture, fat stores remaining at the end of the migratory flight preceding stopover, weather conditions, and fluctuations in daily food supply. Consistent results should nonetheless reflect biologically meaningful differences among estimates (Dunn 2001, Jones et al. 2002).

Two sites had consistently low mass change estimates for spring (Table 3): Last Mountain Bird Observatory and the LPBO site at the extreme end of Long Point in Lake Erie (LPBO-1). Beaverhill Bird Observatory also had a low spring value, but data were available for only one species. Last Mountain Bird Observatory is surrounded by extensive agricultural grassland, and appears to attract birds during spring primarily under unusual weather conditions, rather than serving as a regular stopover site (A. R. Smith pers. comm.). Plant phenology at LPBO-1 is strongly delayed because of the cold spring temperature of surrounding Lake Erie (Dunn 2000, 2001). The only site with consistently low mass gains during fall, Atlantic Bird Observatory, also is affected by cool surrounding water, in this case the Atlantic Ocean, and may experience more fog and high winds than other sites. Birds at this location were heavier early in the morning than birds at other sites during fall, but the predicted reduction in mass gain as a result of higher early morning mass was not enough to explain the low gains at the site.

Among species, the Swainson's Thrush was the only one to have consistently low mass gains during both seasons (Table 4). Dunn (2001) hypothesized that low mass gain for all thrushes at LPBO was a result of poor habitat for ground foragers. At sites other than LPBO, early morning mass of Swainson's Thrushes was up to 9% above lean mass, but again, rate of gain was too low to be explained by this alone.

High relative mass of birds during the early morning probably is an indicator of stopover length. At sites from which birds move on quickly, estimates of mass gain should indicate the true potential for rapid accumulation of mass at the site. Somewhat paradoxically, if birds stay on for more than a day or two at a site that has good food resources, mass gain estimates may be reduced. Heavy birds need not gain as much mass as light ones and, more importantly, may reduce the rate or cease feeding earlier in the day, violating the assumption of the analysis method that there is no bias in time of day that birds of different mass will be captured. This is a topic that needs further investigation.

Mass gain was significantly lower during spring than during fall. Migrants in southern Canada are closer to their final destination during spring and may not need to accumulate as much fuel for continued flight as during fall. However, birds moving northward often carry extra reserves (Sandberg and Moore 1996), and the many instances of spring mass loss in this study suggested that feeding conditions at the study sites often were poor. Temperatures in southern Canada during spring migration can range from near freezing to >20°C, affecting plant phenology and insect activity accordingly, whereas fall weather is much more predictable and benign.

A comparison of mass change at Delta Marsh Bird Observatory during cold versus

warm spring seasons might be a good test of the importance of weather effects. This site stood out as having particularly high mass gains during spring (Table 3), but most of the data came from a series of years with warm, early springs (H. den Haan pers. comm.). In recent years there have been several very late springs, and a comparison of mass change during early versus late seasons would be of interest.

The model of refueling time (Fig. 2) demonstrated some interesting facets of stopover energetics. The shape of the relationship between refueling time and mass gain was little affected by changing assumptions about hours of daily feeding or costs of overnight metabolism and migration, which served mainly to shift the location of the curves in the graphical space. The model showed that the number of hours of gain during the day had an important influence on refueling period (Fig. 2). In both seasons, day length varied considerably among sites, and a single species could experience as much as 3.5 h difference in daylight, depending upon latitude of the site and mean passage date. It is therefore important to consider the amount of daylight that actually is used for feeding.

Limited information in the literature indicated that birds foraged at a high rate during the first 7 h of the day, followed by rest for several hours prior to renewed feeding in late afternoon (Graber and Graber 1983). This pattern corresponds with the experience of banders, who see similar fluctuation in capture rates of migrants. One would expect individual variation in feeding intensity and duration to be great, depending upon factors such as the bird's fuel stores, its motivation to undertake another migratory flight quickly, its need for rest, and conditions of weather and predator abundance, and it is possible that more actively foraging birds have a higher chance of being captured. If that is the case, the data presented here showing that rate of mass gain remains high throughout the day may be biased upwards. The figures shown for refueling times in Table 2 and Fig. 2A should therefore be considered potential periods, while actual periods are likely to be longer. However, they are unlikely to be as long as shown in Fig. 2B, as there is no reason to expect that all birds would cease gaining mass entirely after 7 h of feeding.

The refueling periods described here are not the same as stopover periods. Depending upon factors such as local foraging conditions, weather, body condition, and motivation, birds may undertake a migratory flight of a few hours without waiting long enough to accumulate sufficient fuel to support a full night of sustained migration (Biebach et al. 1986, Moore et al. 1995). Other birds will arrive with some fuel reserves remaining, so will not have to stay in the area for the full refueling period. Stopover also could be longer than the predicted refueling period, as when weather conditions preclude continued migration.

This study was the first in North America to compare mass gain of passerines during migratory stopover across a large geographic area. It examined data retrospectively, however, and the search for patterns was hampered by the fact that data for the same species were not available from all sites and both seasons. Even with similar limitations, however, a similar study of variation in body condition and rates of mass gain along a north-south transect should be able to detect whether there are gradual or sudden changes along the migration route. For example, fall migrants thought to have migrated overland to a study site in southern Mexico had low mean mass, and mass gains were similar to those from this study (Winker 1995). In contrast, birds captured during fall along the central U.S. Gulf coast, and expected to make trans-Gulf flights, were heavier and were maintaining rather than gaining mass (Woodrey and Moore 1997). However, it is unknown whether birds intending trans-Gulf flights gain mass gradually along the migration route, or rely on good conditions for refueling close to the geographic barrier. I sought data from locations in eastern North America to undertake an analysis of mass gain along a migration route, but found there were essentially no data available from the southeastern United States. The alternative is to design a focused study similar to that described by Schaub and Jenni (2000). Results from studies on geographic patterns in mass gain are needed if conservation planners are to make informed decisions on the type and distribution of stopover habitat that should be protected along migration routes.

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MOLT, PLUMAGE ABRASION, AND COLOR CHANGE IN LAWRENCE'S GOLDFINCH

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ABSTRACT.—We examined molting, plumage abrasion, and seasonal color changes of Lawrence's Goldfinch, *Carduelis lawrencei*, to determine to what extent the reported brightening of male colors at the approach of the breeding season results from plumage renewal. Lawrence's Goldfinch has only one molt per year, a complete postbreeding prebasic molt. Color changes during spring result entirely from plumage abrasion and fading, not from a prealternate molt as previously was thought. The yellow breast feathers of the males, but not the females, are unusually resistant to wear, so that the yellow on the breast appears to expand and brighten, as less durable surrounding gray feathers abrade. This may be due to a one-third greater thickness of the rachillae of the yellow barbs in males, so that instead of the rachillae progressively losing yellow-pigmented material, the brown pigmented barbules break off, leaving intact the rest of the barb with only yellow pigment. In contrast, the yellow breast feathers of females abrade progressively at the tips of the rachillae. Females change dorsal coloration little, but males develop a yellowish area on the center of the back, which results when the olive to brown tips overlapping adjacent feathers wear off and uncover yellow proximal portions of neighboring feathers. We point out the need to examine plumage microscopically when studying molting and plumage changes so as not to reach false conclusions about the causes of the changes. *Received 19 December 2001, accepted 20 July 2002.*

As in many passerines, the male Lawrence's Goldfinch, *Carduelis lawrencei*, is more brightly and conspicuously colored than the female, especially during the breeding period (Davis 1999). The functions and evolution of such sexual dichromatism have interested investigators for a long time (Darwin 1874, Hamilton and Barth 1962, Butcher and Rohwer 1989, Savalli 1995). Some species, such as the American Goldfinch, *C. tristis*, increase sexual dichromatism before breeding by molting, whereas others, such as the Snow Bunting, *Plectrophenax nivalis*, do so by feather wear (Chapman 1939, Lyon and Montgomerie 1995). The expense of time, nutrients, and energy during molting probably imposes significant physiological and ecological constraints that must be accounted for in any analysis of the proximate and ultimate causes of sexual dichromatism (King 1980, Walsberg 1983, but see Brown and Bryant 1996).

Published descriptions of seasonal color changes in Lawrence's Goldfinch have been ambiguous. Some authors described the male Lawrence's Goldfinch as having a browner back and hindneck (nape) during autumn and winter, and getting an additional touch of yellow on the middle of the back during summer (Dawson 1923, Edwards 1989, National Geographic Society 1999). Others described the back as being more extensively greenish yellow during winter (Clement et al. 1993), or infused with Spectrum Yellow extending from lower back to the nape during winter, but duller and browner than during summer (Davis 1999; color names that are capitalized are those of Smithe 1974, 1975, 1981). All authors noted that the yellow of the underparts appears more extensive during summer than during winter. The female is similar to the male without black on the head and throat, but duller overall (Dawson 1923) or with a smaller, duller yellow patch on her breast (Davis 1999).

It appears that these color changes result from a body molt during spring, since Lawrence's Goldfinch is reported to undergo a "limited-partial" prealternate molt (Pyle et al. 1997), or an extensive prealternate molt involving all the body feathers (Davis 1999) during March and April. However, in this study we present evidence that color change results instead from feather wear. To characterize the extent and origins of seasonal color change, we quantified the changes of color between winter and summer, and the molting and plumage abrasion throughout the year.

METHODS

Molt and plumage wear.—To determine when molting occurs, one of us (EJW) examined 190 study skins

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TABLE 1. Criteria for determining the molt score of a passerine study skin.

Areas scored	Score	Criteria
Chin, throat, and breast	0	No feathers in any stage of growth are present.
	1	One or more feathers growing on one side only.
	1	One or two feathers growing on the midline.
	2	Three to five feathers growing on or across the midline.
	3	Six or more feathers growing on or across the midline.
Sides and face	0	No feathers in any stage of growth are present.
	1	One or more feathers growing on one side only.
	2	One to five feathers growing on each side.
	2.5	One to five feathers growing on one side, but six or more growing on the other.
	3	Six or more feathers growing on each side.
Crown, back, and rump	0	No feathers in any stage of growth present.
	1	One or more feathers growing on one side only.
	1	One or more feathers growing on the midline.
	2	Three to five feathers growing on or across the midline.
	3	Six or more feathers growing on or across the midline.
Primaries, secondaries	0	No feathers in any stage of growth present.
	1	One or more growing on one wing only.
	2	One or two growing on each wing.
	2.5	One or two growing on one wing, three or more growing on the other.
	3	Three or more growing on each wing.
Rectrices	0	None growing.
	1	One or more growing on one side only.
	2	One or two growing on each side of midline (e.g., 1-1, or 2-2, or left 1 and 3-3, etc.).
	3	Three or more growing on each side.

(see acknowledgments for sources) collected at all times of the year. These specimens had been collected over many years between 1858 and 1972, and represent conditions during a typical calendar year. All but 11 specimens were from the combined breeding and wintering range in California and northern Baja California. The rest were collected during October through December in the extension of the wintering range into Clark County, Nevada, and southern Arizona. We classified specimens according to age characteristics of plumage as HY (in calendar year of hatching), AHY (in second or subsequent calendar year), or U (undetermined age; HY birds that had had a complete first prebasic molt could not be distinguished from older birds; Pyle et al. 1987, 1997). EJW scored molting by examining each specimen under a 7× dissecting microscope, lifting feathers with a dissecting needle to examine their bases and surrounding skin for presence of basal sheaths, pinfeathers, and intermediate stages of feather growth (Willoughby 1986, Willoughby 1991). He counted all feathers in any stage of active growth, assigning scores of 0, 1, 2, and 3 according to criteria in Table 1 to each of these plumage areas: (1) chin and throat—feathers of the interramal, submalar, and anterior two thirds of the cervical regions of the ventral tract; (2) breast—feathers of the posterior one third of the cervical and anterior one third of the sternal regions of the ventral tract; (3) sides—feathers of the abdominal and posterior two thirds of the sternal regions of the ventral tract; (4) face—feathers of the malar, auricular, post-auricular, loral, superciliary, and ocular regions of the capital tract; (5) crown, including forehead, pileum, and occiput, (6) back and rump—feathers of interscapular, dorsal, and pelvic regions of the spinal tract; (7) primaries, (8) secondaries, and (9) rectrices. Adding the scores of all areas yielded a total score for each specimen from 0 (no molting anywhere) to 27 (substantial molting everywhere). This score cor-

related strongly (r = 0.98) with the total number of growing feathers on the specimen raised to the power 0.67. The relationship was described by the equation:

$$\text{Number of growing feathers} = (1.127\ y)^{1.493},$$

where y = molt score. This equation is derived from molt scores and counts of growing feathers of 170 study skins of male American Goldfinches of all ages (EJW unpubl. data). To document patterns of wing and tail replacement, we scored flight feather molt by the method of Newton (1966).

EJW scored each specimen for wear by the method of Willoughby (1986, 1991). Body feathers scored 0 (no wear) when little or no wear was evident, 1 (light wear) when at least one barb lacked up to 1/3 of its original length, 2 (moderate wear) when two or more barbs lacked 1/3 to 2/3 of their original lengths, and 3 (heavy wear) when two or more barbs lacked more than 2/3 of their original lengths. Each plumage area, except face and sides, received the score of the most highly worn 25% or more of the feathers present, or else it received the mean wear score of feathers when two or more wear classes were approximately equally represented in the area, as was common during molting. We assigned scores from 0 through 3 to remiges and rectrices based on the relative amounts of abrasion of barb tips of the longest primaries, the four innermost secondaries, and the rectrices, as illustrated in Willoughby (1991). Adding the scores of all plumage areas gave scores ranging from 0 (no appreciable wear anywhere) to 21 (heavily worn everywhere).

To test for repeatability of molt and wear scores by this method, EJW scored 20 study skins of various fringillid and emberizid finches twice, 7–11 days apart. The mean absolute difference between first and second scores was 0.8 for molt, and 1.3 for wear. Repeating the procedure a second time on five specimens with intermediate molt scores of 9–18, and seven specimens with intermediate wear scores of 6–11, yielded mean coefficients of variation of 10% and 11%, respectively.

Because they have more melanin pigment, males should experience less plumage wear than females (Burtt 1986). Therefore, we compared monthly wear scores of males and females with the Mann-Whitney *U*-test, since these scores are ordinal rather than continuous. We treated each monthly sample as a random sampling of the population, independent of all other monthly samples. Because molt and wear scores of all samples >4, except those at the high end of the scoring scales, passed a Kolmogorov-Smirnov test for normality, we present means with standard errors to indicate central tendency and variability.

Color comparisons.—To assess seasonal changes in coloration, EJW scored a series of 10 male (2 AHY, 8 U) and 8 female (3 HY, 2 AHY, 3 U) skins in fresh plumage, collected September to December, and 13 male and 10 female skins (all AHY) in worn plumage, collected May through July, using the color standards in Kornerup and Wanscher (1978). Criteria for selecting a specimen for scoring were its being in typical adult plumage, the plumage area being free of obvious smudges and stains, and feathers lying smoothly in their natural positions. We converted the Methuen tone designation A through F to numerical equivalent scores 6 through 1, respectively, and compared scores of hue, tone, and intensity between worn and fresh conditions with Mann-Whitney *U*-tests.

Reflectance spectroscopy permits more quantitative and precise color comparison than is possible when comparing with a limited series of color swatches (Smithe 1974). Differences among spectra may appear that are not distinguishable with color swatches, or not visible to the human eye, including differences in the ultraviolet portion of the spectrum. Therefore we obtained reflectance spectra from these same specimens using an Optronic Laboratories OL754 Portable High Accuracy UV-Visible Spectroradiometer with the OLIS-1000 Integrating Sphere reflectance/transmittance attachment, which integrates both diffuse and specular reflectances from the specimen. We measured spectral reflectance from the center of the yellow breast patch, from the center of the back where the yellowish color appears in males, and from the dorsal midline of the anterior back and nape. We exposed an area 1 × 1 cm at the sample port, focusing the source beam on the center of that area, and masking surrounding areas with a white card having a 1-cm^2 cutout in the center. The instrument, calibrated for wavelength accuracy at 546.1 nm, recorded spectral reflectance at 5-nm intervals between 280 and 700 nm, and calculated percent reflectance based on known reflectance of a pressed polytetrafluoroethylene (Teflon™) standard. We extended the range into the ultraviolet (below 380 nm) to see whether there was significant reflection there, as has been observed for various species (Finger and Burkhardt 1994, Andersson 1996). Because of occasional discoloring or disarray, we did not scan all plumage areas on all specimens, which accounts for the various sample sizes presented in the results.

To check for precision of this method, we repeated scans of the breast (five scans), back (five scans), and nape (six scans) of a single specimen, removing and repositioning it at the sample port between each scan. These scans gave standard deviations (SD) at each 5-nm interval ranging from 0.144–2.87 (mean = 1.78) reflectance units. The mean coefficient of variation of all repeat measurements was 13.1%.

For each spectrum, we calculated the Commission Internationale de l'Éclairage (CIE) tristimulus values using the Optronics Laboratories optOLab spectroradiometer operating software. The tristimulus values, X, Y, and Z, represent the amounts of red, green, and blue light, respectively, from a standard source, which when combined produce the same color perception in a standard human observer. These values can be converted to the Munsell color notation system (Hardy 1936, American Society of Testing and Materials 1968, Endler 1990). From the tristimulus values, we calculated the corresponding Munsell color notation using Munsell Conversion, ver. 4.01 (Munsell Color, Gretag-Macbeth, New Windsor, New York).

We compared the mean reflectances of worn and

fresh plumages at all 5-nm wavelength intervals, and compared the CIE tristimulus values derived from the spectra within each sex using independent two-tailed *t*-tests, assuming unequal variances. Since our focus is primarily on the effects of plumage abrasion on coloration, and since males and females clearly differ in appearance, we did not perform statistical comparisons between the sexes.

Feather micromorphology.—During scoring, EJW noted a peculiar form of abrasion of yellow breast feathers in males, but not in females. This prompted us to look for micromorphological correlates of the peculiarity. EJW saved the approximately 0.3 body feathers per bird that separated from the study skins while scoring them for molt and plumage wear. To generate standardized samples for comparison, we used the available yellow feathers from near the center of the breast of five male and four female Lawrence's Goldfinches. For comparison with a species having the typical breast feather wear pattern, we used comparable feathers from five male Lesser Goldfinches (*Carduelis psaltria*), which were part of a separate investigation. Initially we examined and photographed some of these feathers under a dissecting microscope at 7–40×. We then cleaned all the feathers by the method of Laybourne et al. (1992) and mounted each with the outer surface exposed on a 9.5-mm aluminum stub, using Avery "Spot-O-Glue" adhesive tabs (Avery Dennison, Commercial Products Division, Azusa, California). We sputter-coated these with gold-palladium in a Technics Hummer V sputter coater, or with gold in a Denton vacuum sputter coater.

We examined and photographed each specimen at various magnifications in a JEOL Model 5200 scanning electron microscope (SEM), at accelerating voltages of 5 or 10 kV, and a working distance of 20 mm.

We use the terminology for feather microstructure in Dove (1997). To compare measurements of the widths of the rachillae, we calculated mean rachilla width for a specimen measured at four points on the barbs near the tip of the feather, which we designated L1, L2, R1, and R2. These points were positioned as follows: L1 and R1 were on the terminal two barbs 300 μm from the terminal bifurcation, and L2 and R2 were points on adjacent barbs intersected by straight lines perpendicular to the terminal barbs from points R1 and L1, respectively (Fig. 1). We compared the mean measurements of the widths of the rachillae with single-tailed independent *t*-tests, assuming unequal variances, and adjusted probabilities with a sequential Bonferroni procedure when comparing more than two groups simultaneously (Rice 1989, Sokal and Rohlf 1995).

RESULTS

Molt and plumage wear.—AHY birds have one complete molt per year, beginning about the end of July and ending in late October or early November (Fig. 2), with no sign of the prealternate molt described as occurring during March and April (Pyle et al. 1987, Pyle 1997, Davis 1999). Although we looked very carefully for this molt, we saw only a scattering of face and chin feathers in growth on 13 of 30 specimens collected during February and March, and on none of 42 collected during April and May. Such sparse replacement of feathers around the anterior face and chin in a minority of specimens probably represented adventitious replacement rather than traces of molting.

Replacement of remiges and rectrices was simultaneous with body molt, and followed the basic pattern common in passerines (Jenni and Winkler 1994). Most birds replaced rectrices quickly at the same time as remiges, but one bird in October and one in November were molting their tails after remex molt was nearly or quite complete.

Also beginning in late July, HY birds replaced all their body feathers, and some or all of their flight feathers (Fig. 2, Table 2), so that some birds then were indistinguishable from AHY, and could be identified as HY only by collectors' information on the labels. Of 11 specimens that had replaced some but not all primaries, 10 had molted in the eccentric pattern typical of passerines, starting at primaries 4, 5, or 6, and leaving variable numbers of juvenal proximal primaries (Jenni and Winkler 1994, Pyle et al. 1997). The remaining bird had replaced its proximal two primaries (1 and 2), thus having had an arrested descendant molt. Of six specimens that had molted some or all primaries and for which covert molt could be established, three had retained all juvenal primary coverts, and three had replaced them all. However, another bird that had retained all juvenal primaries had molted all its primary coverts. Of 19 specimens that had molted some or all secondaries, and for which molt of greater coverts was determined, 16 had molted all coverts, but three had retained various combinations of juvenal proximal coverts. One specimen had replaced all secondary coverts but had retained all juvenal secondaries.

The wear scores further indicate that no plumage replacement occurred during March and April, as plumage abrasion scores of AHY birds continued to increase throughout the spring (Fig. 2). Female specimens had accumulated significantly higher wear scores

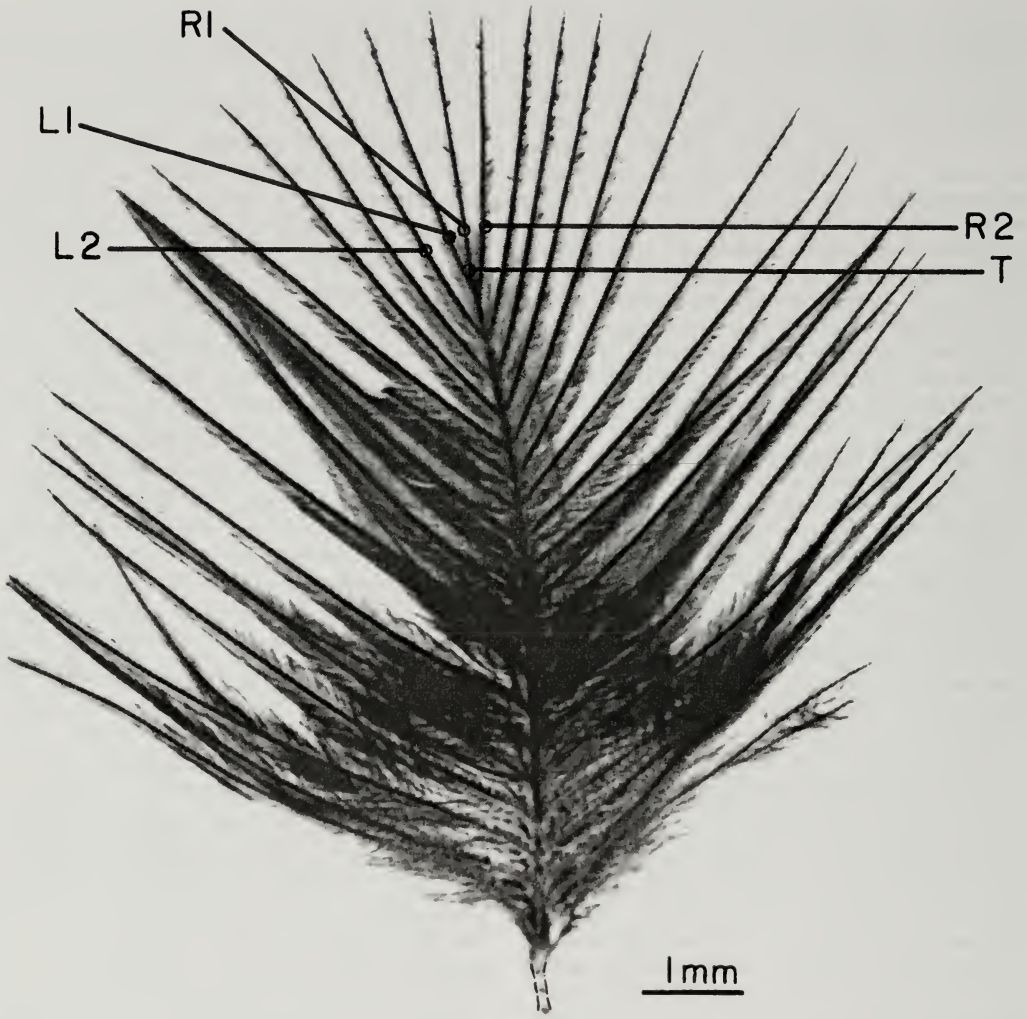

FIG. 1. Negative photographic image of a fresh yellow breast feather from a male Lesser Goldfinch (MVZ117922), to illustrate points on terminal barbs where widths of the rachillae were measured for micromorphological comparisons. Point T indicates the terminal bifurcation at the end of the rachis. Points L1 and R1 lie 300 μm from T.

than males during June ($P = 0.002$) and July ($P = 0.029$). The difference is attributable to higher wear scores on the breast ($P = 0.009$), throat ($P = 0.022$), and crown ($P = 0.003$), but not on the back, wings, or tail. Males are expected to have lower wear scores on crown and throat because of their black pigmentation (Burtt 1986). Contrary to expectation, however, the yellow breast feathers of the males did not progress beyond a wear score of 2, while the surrounding gray feathers reached a uniformly maximum score of 3, as did both yellow and gray breast feathers of females. The dissecting microscope revealed that the rachillae of these feathers abraded little at their tips, but the barbules broke off progressively from tip toward rachis, leaving longer portions of each barb denuded as time passed (Fig. 3b, top). Since our feather abrasion score was based on the relative length of barbs, wear scores stopped increasing once the slender, gray terminal segment, about 1 mm long, had broken off. At the same time, the yellow breast feathers of females, like those of the rest of the body, showed the usual pattern of wear in which the entire barb tip continued to

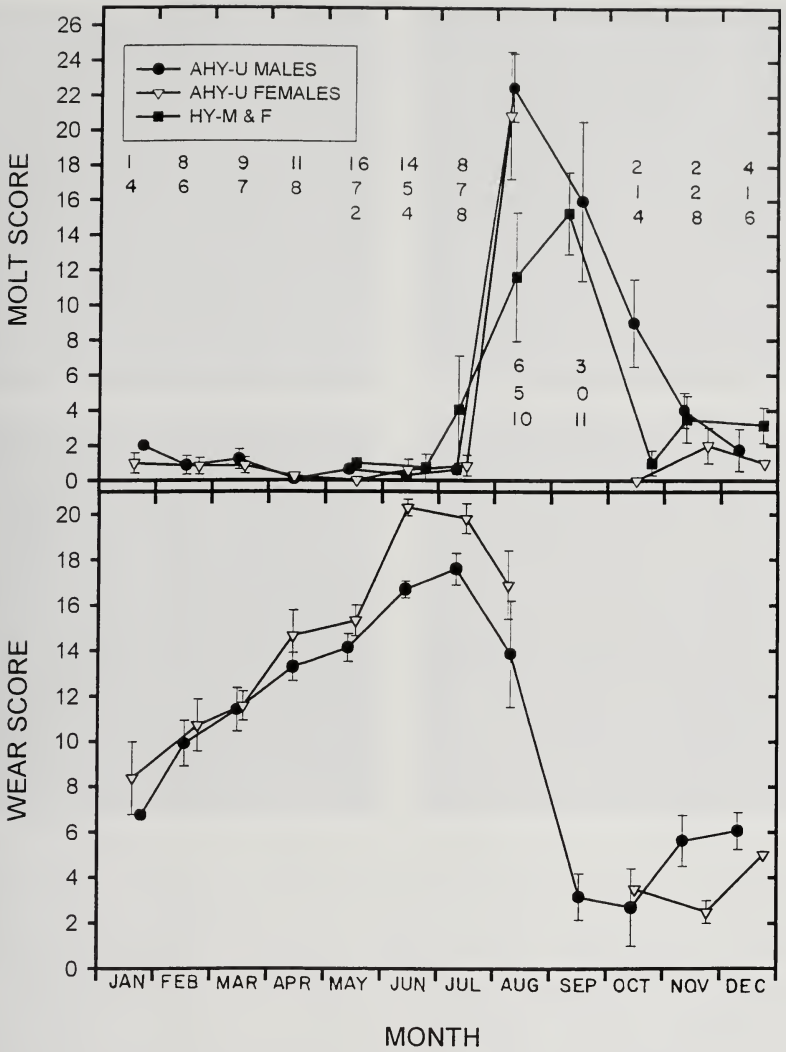

FIG. 2. Monthly molt and wear scores of Lawrence's Goldfinch specimens. Molt scores were elevated only between July and October, showing the period of the single annual molt from August to November, and the absence of molting in February through May before breeding. Mean scores (±1 SE) are plotted on the mean date of collection during the month. The numerals are sample sizes of AHY-U males, AHY-U females, and HY males and females, from top to bottom, respectively.

TABLE 2. Number of individuals (*n*) and percentage of sample of Lawrence's Goldfinch study skins identifiable as HY birds at the end of first prebasic molt, showing that juvenal remiges and rectrices may be replaced completely, partially, or not at all.

	All molted	Some molted	None molted
Primaries	3 (19), 16%	6 (19), 32%	10 (19), 53%
Secondaries	5 (19), 26%	12 (19), 63%	2 (19), 11%
Rectrices	16 (26), 62%	8 (26), 31%	2 (26), 8%

FIG. 3. Scanning electron photomicrographs of typical worn yellow breast feathers of female (a) and male (b) Lawrence's Goldfinches, showing differences in abrasion. The top micrographs show the terminal bifurcation of the rachis and the proximal parts of the terminal barbs, where measurements of rachillae were taken as in Fig. 1. The bottom micrographs show the distal ends of the same barbs. The female feather from USNM202998, 11 November, scored 2 (moderately worn), and shows how the tips of the barbs broke off to produce the characteristically irregular variations in length, while the barbules remained intact to the point where the barb had broken off. The male feather from LACM8469, 16 May, has all barbs of approximately equal length and scored 1 (lightly worn) because less than one third of their original lengths had been lost, despite being worn about eight months longer than the female feather. Unlike the female feather, barbules had broken off, leaving short rectangular stumps (b, bottom), but each barbule tended to break off gradually as shown by the partially abraded proximal barbules (b, top).

break away, progressively shortening each barb without denuding the remainder of its barbules (Fig. 3a, bottom).

Micromorphological correlates of wear.— Under the dissecting microscope we saw that the yellow breast feathers of all males had barbs richly pigmented with yellow carotenoids, with some brown pigment concentrated only around the tips of the barbules. With wear, these brownish barbules broke away, progressively denuding longer parts of the rachillae. In comparison, the yellow breast feathers of the several hundred male American Goldfinches and Lesser Goldfinches we examined in similar studies showed the same progressive loss of barb tips seen in yellow breast feathers of the female Lawrence's Goldfinch. Breakage of barbules in males was concentrated near the tip of the feather, and occurred along most of the distal parts of each barb (Fig. 3b). Where each barbule had broken off was a short, rectangular stump (Fig. 3b). We could see no differences in shape or thickness of the bases of the barbules between

TABLE 3. Median (range) Methuen color scores,[a] with corresponding Methuen and Smithe color names, for adult Lawrence's Goldfinches in fresh and worn plumage, showing that worn males had more saturated breast color, and yellower, more saturated back color than fresh males, whereas worn and fresh females did not differ appreciably in this sample.

Sex, condition	Breast	Back	Nape
Males, fresh (n = 10)	4C7 (4D7-4C8) (brass), 18 Orange Yellow	5F5 (4F4-5F7) (soot brown), 29 Brownish Olive	5F4 (5F3-5F6) (beaver), 29 Brownish Olive
Males, worn (n = 13)	4C8[b] (4D7-4C8) (dark yellow), 18 Orange Yellow	4F7[c] (4F5-4E8) (olive brown), 29 Brownish Olive	5F4 (5F3-5E5) (beaver), 29 Brownish Olive
Females, fresh (n = 8)	4D-E7 (4E6-4D8) (olive brown), 51 light Citrine	5F5.5 (5F5-5F8) (soot brown-Havana brown), 29 Brownish Olive	5F5.5 (5F5-6F8)[d] (soot brown-Havana brown), 119B Dark Drab
Females, worn (n = 10)	4D8 (4E7-4D8) (olive brown), 51 light Citrine	5F5 (5F4-5F6) (soot brown), 29 Brownish Olive	5F6 (5F3-5F7) (Havana brown), 119B Dark Drab

[a] The first numeral denotes hue, increasing from yellow toward red; the capital letter denotes tone from A (lightest) to F (darkest), each letter denoting approximately twice the darkness of the preceding letter; and the last numeral denotes color saturation. Methuen color names from Kornerup and Wanscher (1978) are in parentheses. The approximate color match in Smithe (1975, 1981) is shown by the Smithe color number and name.

[b] Color saturation of worn plumage is significantly greater, $P = 0.034$.

[c] Hue is significantly more yellow, $P = 0.018$, and color saturation is significantly greater, $P = 0.008$, in worn plumage.

[d] The sample size is 7 due to missing feathers on nape of one specimen.

males and females that would explain the difference in wear. Furthermore, we noted that the barbules of males did not break off at any particular place, but abraded gradually from the barbule tip toward its base (Fig. 3b, upper). The rachilla of the male appeared noticeably thicker than those of the female.

Microscopic measurements of the widths of the rachillae of five males (13.2 μm ± 1.3 SE) were significantly greater than those of four females (9.9 μm ± 0.5 SE, $P = 0.035$), and still wider than those of five male Lesser Goldfinches (8.6 μm ± 0.3 SE, $P = 0.015$). The rachillae of the female Lawrence's Goldfinches also were significantly wider than those of the male Lesser Goldfinches ($P = 0.030$).

Color changes.—The series of male specimens we examined showed a yellow breast patch that appeared larger and brighter with the approach of summer. This change and the change in dorsal coloration of the males were well illustrated by Diane Pierce (National Geographic Society 1999:453). Our comparison of male specimens with color swatches in Kornerup and Wanscher (1978) and Smithe (1975, 1981) indicated that as plumage became more worn, the yellow center of the breast appeared significantly more saturated (Table 3), remaining a dark Orange Yellow. The center of the back showed a significant increase in both yellowness and color saturation (Table 3), changing from near Olive Brown or Brownish Olive to a brighter, yellower color, approximating Citrine in several examples. Although the Methuen color scores did not reveal a statistically significant change of color on anterior back and nape, the general impression was of a reduction in tone and color intensity with wear, producing a lighter, grayer appearance in many but not all specimens. This was shown in the upper side of the range of observations, with a Methuen score of 5E5, in Table 3. Females changed much less, without significant changes in apparent color with wear (Table 3).

The apparent enlargement of the yellow area on the breast of the male resulted from abrasion of gray breast feathers surrounding the yellow patch. As these feathers became shorter, they uncovered the edges of the central patch of more durable yellow breast feathers. The increased yellow color of the center of the back resulted from brownish tips wearing off the feathers, exposing the yellow proximal parts of neighboring feathers. Discrete reflectances between 375 and 700 nm from the middle of the yellow breast of males did not change significantly with wear (Table 4), although the Munsell values calculated from the entire spectra indicated a shift toward the slightly greater apparent saturation seen in the

TABLE 4. Color analysis of reflectance spectra of center of breast ("breast"), center of back ("back"), and anterior back and nape ("nape"), showing that in Lawrence's Goldfinches, males get significantly more yellow on back and paler on nape, while females get significantly darker on breast and paler on back as plumage wears.

Sex	Plumage area, condition	*n*	Median wear score[a]	CIE tristimulus value, mean (SE)			Munsell notation, hue value/chroma
				X	Y	Z	
Male	Breast, fresh	9	1	37.7 (1.6)	33.6 (1.5)	5.2 (0.4)	9.23YR 6.30/11.00
Male	Breast, worn	10	1[b]	36.0 (1.4)	31.8 (1.3)	4.6 (0.4)	8.98YR 6.15/11.15
				$P = 0.45$	$P = 0.36$	$P = 0.29$	
Male	Back, fresh	9	1	15.0 (0.5)	13.5 (0.5)	4.6 (0.2)	8.7YR 4.22/5.81
Male	Back, worn	11	3	19.0 (0.6)	17.2 (0.5)	4.8 (0.1)	9.38YR 4.70/6.81
				$P < 0.0001$	$P < 0.0001$	$P = 0.29$	
Male	Nape, fresh	10		15.3 (0.4)	13.8 (0.4)	5.1 (0.2)	8.83YR 4.27/5.51
Male	Nape, worn	11		16.9 (0.4)	15.4 (0.4)	5.8 (0.2)	9.05YR 4.48/5.55
				$P = 0.013$	$P = 0.008$	$P = 0.009$	
Female	Breast, fresh	8	1	33.0 (0.7)	29.9 (0.7)	7.2 (0.5)	9.20YR 5.99/8.89
Female	Breast, worn	10	2.5	29.4 (1.0)	26.5 (0.9)	5.5 (0.3)	9.30YR 5.68/9.06
				$P = 0.011$	$P = 0.009$	$P = 0.015$	
Female	Back, fresh	8	1	14.4 (0.3)	12.8 (0.3)	4.4 (0.1)	8.39YR 4.12/5.72
Female	Back, worn	9	3	18.4 (1.5)	16.7 (1.4)	6.0 (0.6)	8.71YR 4.64/5.96
				$P = 0.029$	$P = 0.026$	$P = 0.041$	
Female	Nape, fresh	8		15.0 (0.3)	13.4 (0.3)	4.8 (0.1)	8.53YR 4.21/5.66
Female	Nape, worn	9		15.6 (0.5)	14.1 (0.5)	5.0 (0.2)	8.74YR 4.30/5.66
				$P = 0.30$	$P = 0.25$	$P = 0.23$	

[a] The nape was not scored for wear, but was at least as worn as the back. Only wear scores of the yellow breast feathers are shown.
[b] Surrounding gray breast feathers scored 3, heavily worn.

Methuen color comparisons. The unworn breast reflected significantly more ultraviolet light than the worn feathers (290–370 nm, $P = 0.033$ to $P = 0.002$). The difference was small, and females showed nearly the same difference, so no sexual dichromatism was evident in the ultraviolet range (Fig. 4). In females, the unworn breast was significantly more reflective than the worn at all wavelengths between 295 and 700 nm ($P = 0.020$ to $P = 0.0002$), indicating that as the feathers abraded, the overall appearance became darker in value, but changed little in hue and chroma (Fig. 4, Table 4). This difference was not enough to be distinguishable with the Methuen color samples (Table 3).

The center of the back of worn males reflected significantly more between 490 and 700 nm (the green through red spectral regions) ($P = 0.008$ to $P < 0.0001$) than of unworn males. This contributed to its distinctly yellowish coloration (Fig. 4, Tables 3, 4). In contrast, wear of the backs of females produced a more variable effect, seen in the greater SE values in Fig. 4 and Table 4, and caused a small but significant increase of reflectance at wavelengths from 340 to 415 nm and 460 to 690 nm ($P = 0.050$ to $P = 0.009$). Thus, color value and chroma both increased slightly (Table 4).

On the anterior back and nape of males, wear produced a significant increase of reflectance between 355 and 700 nm ($P = 0.037$ to $P = 0.0008$), appearing as a paler color, which contrasted more strongly with the black crown. In females, the color of this region did not change (Fig. 4, Tables 3, 4).

DISCUSSION

Our results show that as the breeding season approached, sexual dichromatism became more pronounced: the male's Orange Yellow breast remained bright and expanded in area, and his Olive Brown dorsum became paler, contrasting more strongly with the black of the crown, and gained some yellow on the middle of the back. The female, in contrast, became duller on her breast and slightly paler dorsally. These color changes resulted from plumage abrasion, not from a prebreeding molt.

Molting.—Since we found no trace of a prealternate molt in the specimens we examined, we have to assume that the description of such a molt by others was based on an assumption that the color change prior to breed-

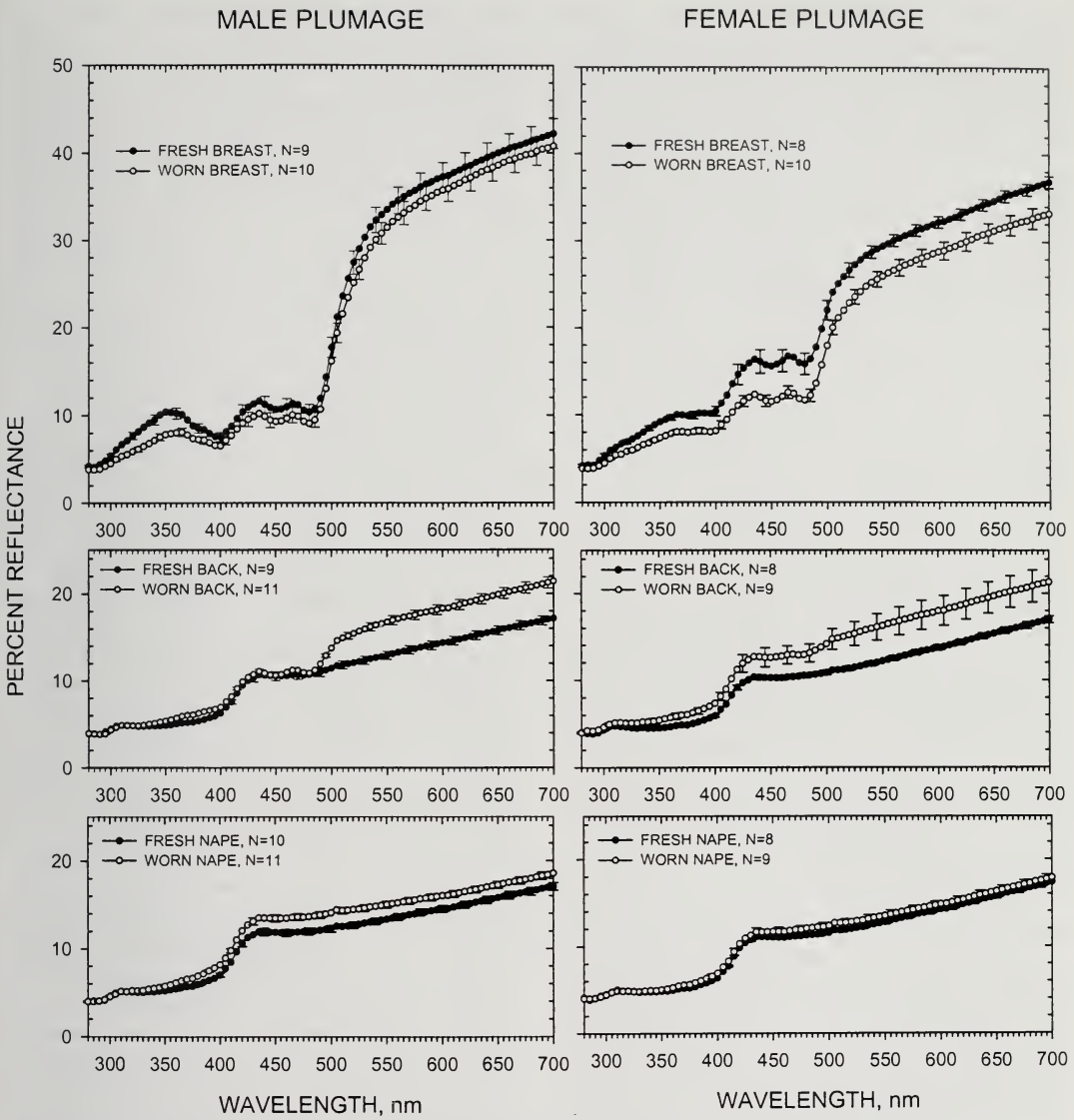

FIG. 4. Reflectance spectra constructed from mean reflectances of fresh and worn plumages at 5-nm intervals on breast, back, and nape of study skins of Lawrence's Goldfinch. Error bars (±1 SE) are staggered at 20-nm intervals for clarity. Worn male breasts reflected significantly less in the ultraviolet, but not in other regions of the spectrum, remaining bright yellow with wear, whereas worn female breasts reflected significantly less at nearly all wavelengths, becoming darker with wear. Worn male backs reflected significantly more in the green through red, becoming distinctly lighter and more yellow, whereas worn female backs reflected more in all visible wavelengths, so they became lighter but stayed nearly the same color. Worn male napes reflected significantly more in all visible wavelengths, becoming lighter, whereas female napes hardly changed with wear.

ing results from a molt. However, such a molt would be exceptional, because of the rarity of prebreeding molts within the Carduelinae. The American Goldfinch is the only cardueline species known to have an extensive prealternate molt that produces a change of color (Middleton 1977, 1993). The American Goldfinch and Lesser Goldfinch are the only ones of 124 cardueline species reported unambiguously to have a prealternate molt that replaces most or all of the body feathers (Newton 1972, Clement et al. 1993, Middleton 1993,

Watt and Willoughby 1999). Therefore, finding such a molt in this or any related species would be unusual. Our results confirm that Lawrence's Goldfinch is comparable to the great majority of carduelines in having only one molt per year, a prebasic molt. When a cardueline does have a prealternate molt, it typically is of limited extent and does not change coloration. We advise investigators to examine specimens closely for evidence of molt, under a microscope when possible, to avoid coming to false conclusions. Such mistakes can distort the results of hypothesis testing procedures that rely on the accuracy of natural history data (e.g., studies of Rohwer and Butcher 1988, Butcher and Rohwer 1989, and Badyaev 1997a).

The great variation in the pattern of molting of primaries, secondaries, and their coverts during the first prebasic molt in our small sample is remarkable. Among species for which similar data are available, it appears closest to the Siskin (*Carduelis spinus*), which showed similar great variation among the small proportion of birds that had molted any primaries (Jenni and Winkler 1994). However, Lawrence's Goldfinch more frequently replaced primaries, and had even more variation, such as replacing juvenal primary coverts but not primaries.

Morphological correlates of color enhancement.—The peculiar thickness of the rachillae of the yellow breast feathers of males (Fig. 3) appears to be the reason that these feathers, by resisting wear and color loss, maintained their ability to provide a brightly colored patch that expanded in area with the approach of the breeding season. Morphological differences correlate with presence of carotenoid pigments in a variety of birds (Brush and Seifried 1968). The related Common Redpoll (*Carduelis flammea*) and Purple Finch (*Carpodacus purpureus*) have carotenoid-containing feathers that are modified such that they enhance exposure of the pigmented parts. This modification consists of a reduction in melanin pigmentation, elimination of barbules, and flattening of the barb, which increases the pigmented area exposed to view (Brush and Seifried 1968). The male Purple Finch, in particular, loses the barbules on its red crown feathers at the time its coloration brightens with approach of spring, while the barb tips wear very little (Dwight 1900). These barbs become progressively denuded of their whitish barbules as the plumage becomes less hoary and brighter red in appearance (Dwight 1900). The breast feathers of the male Lawrence's Goldfinch therefore resemble the crown feathers of adult male Purple Finches in the way they wear.

General comments.—It is noteworthy that the three North American goldfinches and the Pine Siskin, judged in a recent analysis to be phylogenetically more closely related to each other than to any other member of the genus (Badyaev 1997b), demonstrate a full range of variation in sexual dichromatism and annual molt cycles. The Pine Siskin (*Carduelis pinus*), at one extreme, has no sexual dichromatism, and a single annual molt (Dawson 1997, Pyle et al. 1997). In the American Goldfinch, at the other extreme, males alternate between a dull, female-like nonbreeding plumage and a bright, highly sexually dichromatic breeding plumage through alternation of a complete prebasic molt and an extensive prealternate body molt (Middleton 1993). The Lesser Goldfinch is variable with respect to molting. It is sexually dichromatic and keeps the same appearance all year, but those of the Pacific coast states and Baja California have a single annual molt, whereas those of the interior states and the rest of Mexico have two complete molts per year (Watt and Willoughby 1999). The Lawrence's Goldfinch, as demonstrated here, is sexually dichromatic all year, but becomes more so during the breeding season, not by a molt, but by feather abrasion. These observations indicate that variations of sexual dichromatism and molting cycle are not phylogenetically constrained in this group, and suggest that such variations may have evolved quickly and repeatedly within different lines of descent. Because all four species have ranges that overlap in California and Baja California and except for Lawrence's Goldfinch, have extensive overlap of ranges elsewhere, they should be a fertile group for investigating the roles of ecological, physiological, and behavioral factors influencing the evolution of both sexual dichromatism and molting cycles.

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VARIATION IN CAROTENOID-BASED COLOR IN NORTHERN FLICKERS IN A HYBRID ZONE

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ABSTRACT.—We studied variation in the carotenoid color of flight feathers of hybrid Northern Flickers (*Colaptes auratus*) and its correlation with reproductive performance and survival. Color scores provided by a digital camera revealed in 218 individuals a continuous spectrum from yellow to red. Males tended to be slightly redder than females. Within individuals, an analysis of color change with age revealed that males, but not females, became redder with age. Except for yearling females, body condition did not improve with age, suggesting that color is not linked to body condition measured during incubation. We did not detect any correlations between feather color and measures of reproductive performance, such as clutch size, hatching success, or fledging success, or return rate to the study area. In a hybrid population where intraspecific variation in color is controlled partly by genes, hue or brightness may not be a useful signal of individual quality, contrary to other studies of birds. About 25% of flickers had one or more tail feathers that differed from the rest of the plumage. In each case, the "odd" feathers were paler or yellower in color and may have been caused by diet or stress when the feathers were lost and regrown during winter. Such odd colors support the hypothesis that red carotenoid pigments are costly to maintain under stressful conditions. *Received 25 January 2002, accepted 5 August 2002.*

"The flicker situation will puzzle all the naturalists in the world" (Audubon 1843:71).

Documentation of variation in plumage color, whether across a species' range or within a population, has been the foundation for many subdisciplines in ornithology. Trends in coloration are the raw material in avian systematics, allow us to describe the demography of populations, and more recently in behavioral ecology, reveal the power of sexual selection in shaping bird morphology (Hill 1991, Gray 1996). In general, males are more brightly colored than females, and juveniles have a drab appearance compared to adults (Butcher and Rohwer 1989). Bright colors in birds may function in numerous ways as signals to conspecifics or predators (reviews in Burtt 1981, Butcher and Rohwer 1989, Savalli 1995, Fitzpatrick 1998). Of particular interest in recent years are the bright yellows, oranges, and reds, so common in the feathers of birds, that are a product of carotenoids. These pigments are of such interest because the same molecules have a variety of important physiological functions related to the health of birds (see Lozano 1994, Olsen and Owens 1998, Möller et al. 2000). In this paper, we examine intrapopulation plumage variation in the Northern Flicker (*Colaptes auratus*), a woodpecker with extensive and conspicuous carotenoid pigmentation on the undersides of the flight feathers of both the wing and tail. Two subspecies (formerly species) are recognized: *C. auratus auratus*, the Yellow-shafted Flicker of eastern North America and the Great Plains, and *C. a. cafer*, the Red-shafted Flicker of western North America. As the common names suggest, the color of flight feathers is yellow or red and has a genetic basis (Short 1965, Moore 1995). The two subspecies groups hybridize along a zone extending along the Rocky Mountains from Texas to Alaska; birds with an intermediate feather color, shades of orange, are identified as hybrids (Moore 1995, Wiebe 2000).

The bright colors of the flight feathers of the Yellow-shafted Flicker are derived from three carotenoids that are absorbed untransformed from the diet: lutein, zeaxanthin, and β-cryptoxanthin. In contrast, the colors of the Red-shafted Flicker are derived from oxidation of ingested carotenoids such that the predominant pigments are astaxanthin, adonirubin, α-doradexanthin, and canthaxanthin (Stradi 1998). In a previous study (Wiebe and Bortolotti 2001), we examined the frequency of yellow-orange-red color morphs in a hybrid population by using color scores from a digital camera.

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Relationships between color and individual traits have not been examined in flickers; however, the potential role of color in communication is suggested by ritualized displays during which both males and females fan their wings and tails and expose the colored undersides of their flight feathers in exaggerated motions (Moore 1995). The display may be directed either to a member of the same sex, in which case it probably is agonistic, or to the opposite sex, in which case it may function in mate choice. Thus, it is not implausible that color variation may be used to select an appropriate mate either with regard to species, or in selection of a high quality partner. In the latter case, it is predicted that color may correlate with traits such as age and body condition.

In a hybrid zone, correlations between color and reproductive success are especially interesting. If a wide range of color variation is controlled by genes in a hybrid zone, it may be a poor signal of age or experience. On the other hand, if the fitness of hybrids is higher or lower than parental types in the hybrid zone, color could be an excellent indicator of potential fitness. The leading hypothesis for the stability of the hybrid zone in flickers is that hybrids have higher fitness than pure types in the hybrid zone (Moore and Buchanan 1985). Therefore, orange flickers should have greater success than yellow or red birds there. Despite potential fitness differences among flickers of different colors related to their genetic makeup, most previous studies have failed to detect mate choice according to color (Bock 1971, Moore 1987, but see Wiebe 2000). In this paper, our aim is not to test the function of color, but to examine proximate correlates of color variation such as age, sex, body condition, reproductive success, and return rates of adults. It is our hope that this baseline information will be useful in future studies that may focus on the adaptive significance of color variation in Northern Flickers.

METHODS

Study site and field methods.—The study area near Riske Creek, in central British Columbia (51° 52′ N, 122° 21′ W) within the hybrid zone of Northern Flickers, encompassed approximately 75 km^2 of grassland with scattered patches of trembling aspen (*Populus tremuloides*) and mixed coniferous forest (Martin and Eadie 1999). Flickers were observed during 1998 and 1999 from the time they arrived on territories during late April until the young fledged during late July. Potential territories and peripheral regions were searched intensively every 2–3 days during spring using tape-recorded calls. Because the habitat was fairly open and flickers were responsive to the tapes, we believe nearly all nesting birds were located. We also trapped most birds each year (see below) to estimate return rates. During 1998, 111 breeding adults were banded, of which 36 returned in 1999. As we detected only one bird from 1998 in 2000 but not in 1999, we are confident that we detected most color-banded birds (36/37 = 97%) if they returned and therefore our return rates are an accurate measure of local survival.

Adult flickers were trapped at the nest either by stuffing the nest hole during incubation, or by pulling a net over the hole with an attached string during brood rearing (see Wiebe and Swift 2001). We trapped ≥96% of nesting adults each year, and there is no reason to think trapping success was biased according to plumage color. Flickers were aged as 1, 2, or 3 years old by molt of upper primary coverts (Pyle et al. 1997) but for some analyses we used two age classes by combining all birds ≥2 years as "adults." We entered six body size measurements, bill length, bill depth, wing chord, tarsus, central rectrix, and ninth primary length, in a principal components analysis and used the first component (PC1) as a measure of overall body size (Rising and Somers 1989). Because of sexual dimorphism, we performed separate analyses for each sex and made PC1 values positive by scaling them to a hypothetical individual of zero size (Bortolotti and Iko 1992). The third rectrix on the right side was collected from each adult flicker when it was trapped in May or June, and saved in a paper envelope to be photographed later. If the individual had multiple colors in its tail, we collected two feathers.

Determining color.—Quantifying subtle variation in feather color is difficult because observers' perceptions depend upon the context, the degree of illumination, and individual differences (Endler 1990). Previous studies of flicker subspecies ranked the color of feather shafts and vanes into 3–5 categories (Short 1965, Bock 1971), or named the feather vane color according to standardized color chips (Test 1940). Such categories are too coarse for many questions. In a previous paper (Wiebe and Bortolotti 2001), we used a digital camera to measure color on a continuous scale (Villafuerte and Negro 1998). A Nikon Coolpix E900s digital camera was used to photograph each rectrix. We photographed all feathers during November 1999 alongside two gray scale reference cards so that we could adjust colors to control for differences in illumination (Villafuerte and Negro 1998). Although the camera did not record UV reflectance, we do not believe this was a serious drawback as carotenoids reflect light mainly in the visible range, and red tail coverts of the Great Spotted Woodpecker (*Dendrocopus major*) did not show UV reflectance (Burkhardt 1989).

To derive a single color variable, we plotted feathers on the red and blue brightness axes provided by the

camera. That scatter plot revealed that a single axis (e.g., the "red" axis) was not sufficient to distinguish color hues perceived by us. Rather, color hues were segregated in tight diagonal bands across both axes. We used the reduced major axis technique to fit a regression line through the median red and blue values and then used residuals from this regression as the new single color variable (Wiebe and Bortolotti 2001). These color residuals corresponded well to a scale of paint chips ranked from yellow through orange and red; higher residuals indicated more reddish feathers and lower residuals indicated yellow hues. Wiebe and Bortolotti (2001) also confirmed that feather hues as ranked by human test subjects matched the ranking of the feather color residuals as calculated by us.

Statistical analyses.—We analyzed body size because the Red-shafted Flicker was reported to be larger than the yellow-shafted subspecies (Moore 1995) and also because body size may influence social dominance and territory acquisition, and therefore quality of the individual. As an index of body condition, we used the residuals of a reduced major axis regression of body mass on PC1 (Green 2001). We recaptured 27 flickers during 1998 and 1999. To avoid pseudoreplication in analyses involving color frequencies and reproductive performance, we randomly chose one observation per individual in the dataset except when analyzing within individual variation. For analyses of return rates and changes in body condition within individuals between years, recaptured birds from 2000 were included. We performed statistical analyses using SPSS, and all tests were two tailed. Means are reported ± SE. Initial ANOVA models included all higher order interaction terms, but in order to increase power these were dropped from the model if nonsignificant.

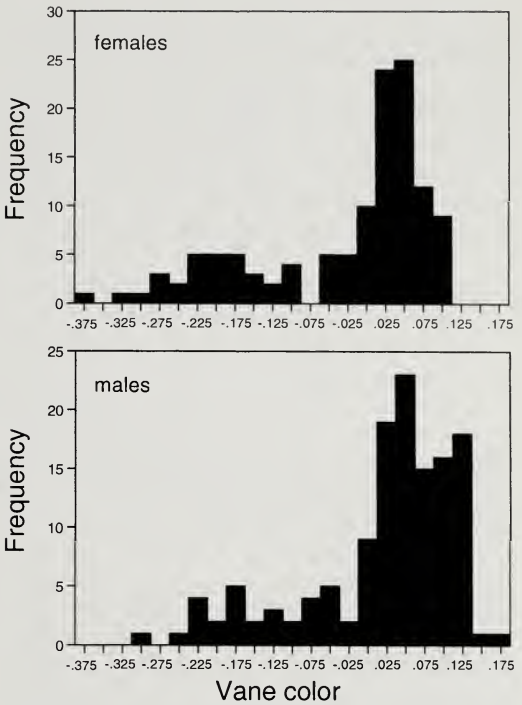

FIG. 1. Distribution of color scores in the hybrid flicker population at Riske Creek, British Columbia, 1998–2000, as determined with a digital camera. Males were redder than females as shown by the greater frequency of higher (positive) color scores.

RESULTS

Not counting "odd" colored feathers but including recaptures, we collected and photographed 245 flicker tail feathers: 111 from 1998 and 133 from 1999. Using the reduced dataset with one feather per individual, a three-way ANOVA revealed no significant effect of year ($F_{1,213} = 0.12$, $P = 0.72$) or age (ages 1–3; $F_{2,213} = 0.56$, $P = 0.57$) on feather color but a significant sex effect ($F_{1,213} = 4.6$, $P = 0.032$). After pooling years, males were slightly more reddish ($n = 107$, mean color residual = 0.0064 ± 0.01) than females ($n = 111$, mean color = −0.026 ± 0.01; Fig. 1). For both sexes, the modal color in the population was about 0.05, a dark orangish red (approximately the "Chrome Orange" of Smithe 1975).

A fraction of individuals trapped during spring during the two years (22% of 114 females and 25% of 105 males) had one or more flight feathers that differed conspicuously in color from the majority of their rectrices and primaries. In the tail, these odd feathers often were shorter or stunted, but not more worn compared to other feathers, suggesting they had been lost and regrown after the normal period of postbreeding molt during the fall. One third of these odd feathers had a "washed out" appearance, (i.e., pale pink or pale yellow), but 66% of odd feathers were still of a vibrant hue, but yellower. The shift in color was sometimes extreme; "red-shafted" flickers could have a feather almost as yellow as typical yellow-shafted *C. a. auratus* birds. In one case, a bird was bilaterally asymmetrical with one entire side of the tail red and the other yellow. Paired *t*-tests confirmed that such regrown feathers were significantly yellower ($t_{15} = 4.13$, $P = 0.001$; Fig. 2). Of 19 birds with odd feathers that were trapped in two consecutive years, only four (21%) had odd feathers in both years, which was expected based on the overall frequency of odd

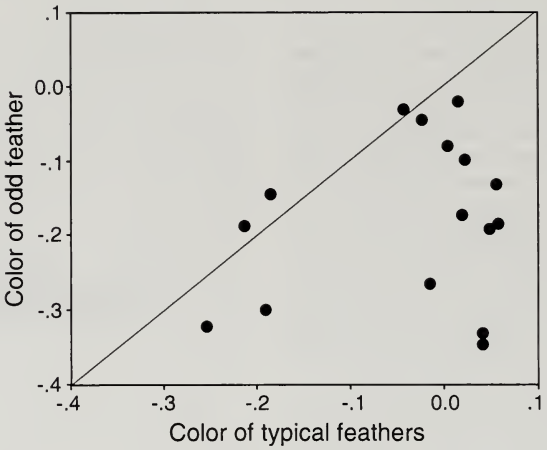

FIG. 2. The color of odd feathers and typical feathers collected from an individual flicker's tail at the same time, Riske Creek, British Columbia, 1998–2000. A shift to yellower hues in the odd, regrown feathers is shown by points below the diagonal line.

feathers in the population. In these four individuals, the odd feather in the tail was at a different location each year. It also is clear that replacement feathers did not always grow in as a different color. Nine adults that were retrapped on the study area in July (i.e., after their extracted tail feather had begun to regrow), had replacement feathers that were indistinguishable to our eye from the older rectrices.

For age-related changes in color within individuals, we used paired *t*-tests to compare feathers of individuals trapped in both years. With all ages pooled, there was no significant change in color with age for females (t_{11} = 0.29, P = 0.78; Fig. 3a) but a significant increase in redness for males (t_{15} = 2.92, P = 0.014; Fig. 3b). This age effect was not simply a product of a change in age class (i.e., from first to second year), as the relationship was still significant when only males two years of age and older were analyzed (t_7 = 2.4, P = 0.044). The degree of color change with age (mean difference in residual = 0.045 ± 0.06) was not as marked as the differences in color with odd regrown feathers (mean difference 0.14 ± 0.13; compare Figs. 2 and 3).

Color was not associated with our measures of individual quality. There was no association between PC1 and feather color for either males (r = 0.03, n = 107, P = 0.75) or females (r = −0.02, n = 111, P = 0.82). Because color extremes had a genetic basis in the population, simple correlations between color and body condition at the population level may have little value. Instead, we analyzed longitudinal changes in body condition with age to test whether the increase in redness with age (see above) might be explained by a proximate mechanism of an increase in body condition. Including recapture data from 2000 and pooling all ages, body condition measured during incubation improved with age for females (paired-t_{29} = 2.83, P = 0.007) but not males (paired-t_{39} = 0.68, P = 0.58). Thus, within each gender, any changes in body condition with age did not correspond with an increase in redness with age.

With respect to reproductive performance, color was not associated with clutch size (r_s = 0.05, n = 216, P = 0.54) in the hybrid population and feather color was not related to the number of nestlings that eventually fledged (r_s = 0.03, n = 212, P = 0.73). Thirty-six of 111 (32%) individuals examined in 1998 returned to the study area in 1999, and 41 of 134 (31%) from 1999 returned the subsequent year. Return rates did not differ significantly between years (χ^2_1 = 0.10, P = 0.83) or between sexes (χ^2_1 = 1.4, P = 0.27). Color did not differ significantly between birds that returned and those that did not (t_{243} = 1.1, P = 0.23).

DISCUSSION

Color in relation to age and sex.—Unlike many species of birds that have bright plum-

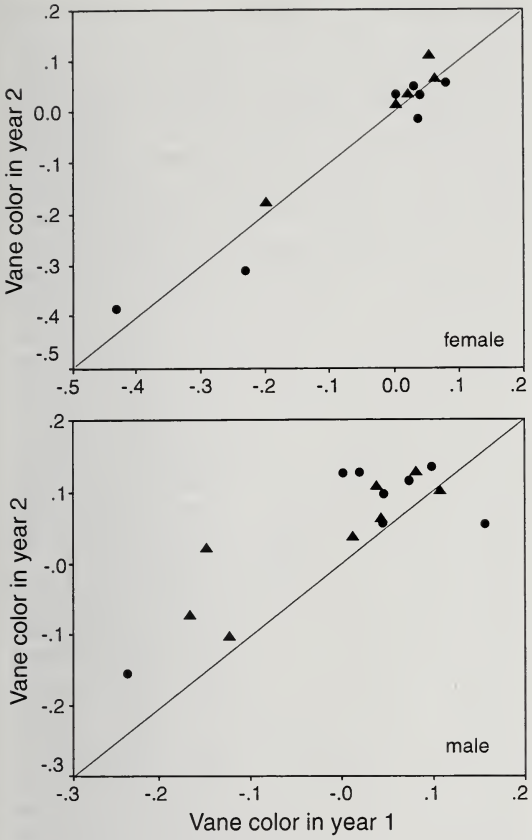

FIG. 3. A longitudinal comparison of feather color in Northern Flickers as they age from one year to the next, Riske Creek, British Columbia, 1998–2000. Circles indicate yearlings and triangles indicate birds >2 years old. The feathers of males but not females became redder with age as shown by the position above the diagonal line.

age (Butcher and Rohwer 1989, Gray 1996, Badyaev and Hill 2000), carotenoid-based coloration in flickers does not play a major role in variation with regard to age or sex. Instead, the melanin-based malar stripe is important for sex recognition (Noble 1936). The brighter red score of males in our population of hybrids (Fig. 1) could be merely the result of different proportions of individuals of each sex along the hybrid continuum, rather than a difference related to the biology of the sexes. The fact that only males became redder with age (Fig. 3) may explain how the difference arose in mean coloration between the sexes. However, the relatively subtle shifts in color with age means that it is not possible to age flickers in the field based on color. Villafuerte and Negro (1998) also found a subtle difference between the brightness of captive male and female Red-legged Partridges (*Alectoris rufa*) that was revealed only by a digital camera. A sex difference in age-related carotenoid coloration also has been reported for American Kestrels (*Falco sparverius*; Bortolotti et al. 1996).

Color variation and reproductive performance.—Subtle variation in color within an age class or sex is of interest because it may indicate a bird's quality as measured by body condition, immunocompetence, or survivorship (Hill and Montgomerie 1994, Bortolotti et al. 1996, Nolan et al. 1998, Hill 2000, Lindström and Lundström 2000, Hõrak et al. 2001). We did not find any evidence that body condition, reproductive output, or return rate varied along the color spectrum in a hybrid flicker population. In contrast to our results, redder male Northern Cardinals (*Cardinalis cardinalis*) obtained higher quality territories and produced more offspring than paler males (Wolfenbarger 1999). Redder male House Finches (*Carpodacus mexicanus*) had higher provisioning rates to nestlings and higher survival (Hill 1991, Nolan et al. 1998). However, the genetic basis of color variation in this hybrid population complicates the analysis and interpretation of potential relationships with condition. While it still is plausible that flickers within the core range of the pure subspecies may show subtle variation in color that functions in social situations (e.g., mate choice), the reliability of color as an honest signal of quality may have been compromised in the hybrid zone.

The second aspect of color that complicates our analysis is that the variation we observed is unlike that of most populations of birds. In other species, the size of the carotenoid-based color patch (Hill 1993) or the intensity of hue along a gradient of dull to bright (Bortolotti et al. 1996, Wolfenbarger 1999) is quantified. In such studies, brighter birds likely had more circulating carotenoids, which in turn may explain why there was a correlation between color and health (Lozano 1994). In contrast, flickers varied along a continuum of hues from bright yellow to bright red, displaying different, but not necessarily more, carotenoids. Instead, our find of yellow odd feathers

is consistent with the hypothesis that the expression of red pigments *per se* is costly (Hill 1996, 2000).

Regardless of any potential signaling functions, the leading hypothesis about the flicker hybrid zone suggests there should be a relationship between color and reproductive performance (Moore and Buchanan 1985, Wiebe and Bortolotti 2001). However, we did not find support for the idea that intermediate phenotypes performed better in terms of reproduction than parental types in the hybrid zone, and return rates to the study area were not associated with color. Similarly, with a smaller sample size and categorical classification of phenotypes, Moore and Koenig (1986) did not detect differences in clutch size within a hybrid population in the central United States.

Causes of odd-colored rectrices.—In many species, the brightness of carotenoid colors may be influenced by a number of environmental factors. Since birds must obtain carotenoid molecules from their food, and they grow pale feathers on artificial diets lacking carotenoids (Brush 1978), different diets in the wild have been implicated in intraspecific variation (Slagsvold and Lifjeld 1985, Hill 1992, Eeva et al. 1998). However, the idea that carotenoids are limiting in the wild is controversial (Hudon 1994, Thompson et al. 1997, Bortolotti et al. 2000). Instead, physiological capabilities to absorb and use carotenoids in the diet may be influenced by physical condition, stress, or degree of parasitism (Weber 1961, Thompson et al. 1997). Gender, age, and seasonality influenced circulating carotenoids and color in American Kestrels even when diet was controlled (Bortolotti et al. 1996, Negro et al. 1998).

Surprising to us was the high prevalence (nearly 25%) of flickers with odd colored feathers in their wings or tail. Fading in sunlight does not change the hue of flicker feathers (Wiebe and Bortolotti 2001). Odd feathers must be explained by differences in diet or physiology (or both) at the time the feathers were regrown compared to conditions during the normal period of postbreeding molt from August to October. Feathers pulled in May and examined in July matched the normal color of the other rectrices. This suggests that there is a seasonal window, at least between May and October, during which carotenoids were deposited in feathers in a typical color for the individual. Pale pink or pale yellow feathers also occur in nestling flickers, which often share the nest with normal, brightly colored siblings. Such uniformly pale chicks often are the smallest of the brood (KLW pers. obs.), but probably receive the same types of food items as bright siblings. Therefore, paleness in nestlings appears to be caused by a general lack of food and poor health rather than different dietary items. We can not rule out seasonal diet changes as a cause of pale feathers in adults because the diet of flickers shifts from nearly 100% insect prey (ants) during summer, to mainly fruits and seeds during winter (Beal 1911, Test 1969). However, many fruits contain abundant carotenoids (Gross 1987), so it is more probable that pale, regrown feathers indicate greater energetic or physiological stress during winter.

It is more difficult to explain odd feathers that were still bright, but yellower than normal. Red flickers grew odd bright yellow feathers, but yellow birds never grew odd red feathers. Test (1969) also reported flickers with mixed plumages but was not clear whether these were red-shafted individuals growing yellow feathers or vice versa. It is well documented that diverse avian taxa are capable of metabolic conversion of ingested carotenoids into other forms (Goodwin 1984, Brush 1990). Red-shafted Flickers have a biochemical pathway, probably lacking in yellow-shafted individuals, which oxidizes yellow carotenoid pigments into red ones (Stradi 1998). Such biochemical pathways may be costly (Hudon 1991, review in Hill 1996) and the amount of yellow carotenoids converted to red ones may depend upon a bird's physical condition. For example, male Eurasian Bullfinches (*Pyrrhula pyrrhula*) experimentally fed a constant amount of yellow pigments produced brighter red feathers when given an energy rich diet (Schereschewsky 1929). If Red-shafted Flickers are energetically stressed during winter, costly pigment conversion may be limited, causing feathers grown during winter to be yellower than normal. Test (1969) found that Red-shafted Flickers fed ground carrots in captivity produced orange feathers. Psychological stress associated with being held in captivity may reduce the expression of red pigment in birds even though carotenoid rich

diets are provided (Weber 1961 cited in Hudon 1994).

Plumage color has been a basis for the classification of flicker subspecies, but our study suggests caution is needed because there are nongenetic components to color variation. For example, Short (1965) interpreted "off-color" feathers reported by Test (1942) as indicators of hybridization. However, odd-colored feathers within a bird's tail probably result from environmental or physiological effects during feather molt rather than mixed parentage. It seems that a wild flicker with uniformly orange flight feathers is likely a hybrid, but the orange color of flickers raised in captivity could indicate stress rather than hybridization. The subtle differences in redness associated with age and sex probably are not large enough to influence classification based on human perception. Further study is needed to determine whether such subtle differences predict reproductive performance in pure parental populations.

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Short Communications

Wilson Bull., 114(3), 2002, pp. 401–403

First Reported Case of Classical Polyandry in a North American Woodpecker, the Northern Flicker

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ABSTRACT.—During a study of Northern Flickers (*Colaptes auratus*) nesting in central British Columbia, I discovered a polyandrous female attending two nests 447 m apart. The phenology at the two nests was staggered so that the female took incubation shifts and fed nestlings at both trees. Hatching success was typical but the female appeared to divide her provisioning effort between the broods. At one nest, only about 20% of visits were by the female, compared to a typical rate of 50%. Polyandrous mating benefited the female, who fledged all six nestlings in one brood and all seven in the other. The mean number of fledglings for monogamous females in this population was 5.9. Two other cases of polyandry possibly related to human disturbance are discussed. These results suggest exceptions to the idea that, in Picidae, the full contribution of both genders during incubation and brood rearing is required to fledge young. *Received 1 October 2001, accepted 5 June 2002.*

Classical polyandry is a mating system in which a single female mates either sequentially or simultaneously with more than one male during a breeding season while males mate with no more than one female. In addition, each male has his own nest and cares for his own young (Oring 1982, 1986; Ligon 1993). Bird species practicing classical polyandry are rare, most examples being within the order Charadriiformes (Ligon 1993). Most woodpeckers, family Picidae, are socially monogamous (Short 1982, Cramp 1985) although 2 of the 22 North American woodpecker species have unusual mating systems: cooperative breeding in the Red-cockaded Woodpecker (*Picoides borealis*) and Acorn Woodpecker (*Melanerpes formicivorus*), and also polygynandry in Acorn Woodpeckers (Ligon 1970, Walters et al. 1988, Koenig et al. 1998). Here I report a case of classical polyandry in the Northern Flicker (*Colaptes auratus*), a species which typically is monogamous (Moore 1995).

I studied Northern Flickers during 1998–2001 at Riske Creek, British Columbia, Canada (51° 52′ N, 122° 21′ W). For details of the study area see Wiebe (2000, 2001) and Martin and Eadie (1999). Each year, reproduction at 80–90 nests was monitored closely and >95% of adults on the site were color banded for individual identification. Two bands were placed on each leg and an individual bird was known by four letters standing for its color combination. Trapping methods and details about reproduction and morphology are in Wiebe and Swift (2001) and Wiebe and Bortolotti (2001).

I discovered the case of polyandry when female RAGG, known to have incubated at Nest A with male AGKG, was recorded on videotape on 14 June performing incubation duties at Nest B (447 m from Nest A) with male BAKG (Fig. 1). The first nesting attempt of male BAKG that season had been at Nest C and had failed about 28 May after he was evicted by European Starlings (*Sturnus vulgaris*). His original mate, female BAKY, was not seen again and he renested with RAGG who laid her first egg at Nest B on 4 June (Fig. 1). While laying eggs in Nest B, RAGG continued daytime incubation shifts at Nest A. Chicks at Nest A hatched on 8 June and RAGG then spent most of her time incubating at Nest B until the chicks there hatched on 20 June. Between 20 June and 2 July, RAGG fed chicks at both nests but accounted for only 2 of 12 feeding visits at Nest A (8 h of observation over 3 days). At Nest B during one day (14 h) of filming, she fed the chicks on 6 of 23 visits. All six chicks that hatched at Nest A fledged on 5 July and all seven chicks fledged from Nest B on 14 July.

Classical polyandry is rare in Northern Flickers. With intensive nest monitoring and

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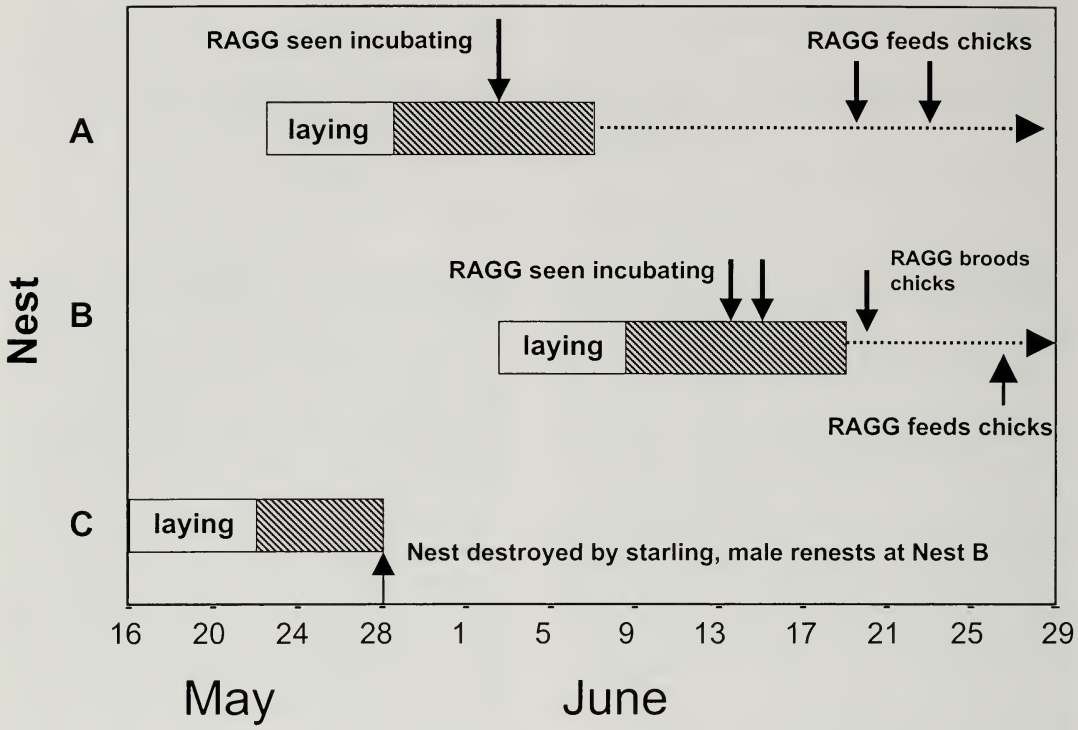

FIG. 1. Reproductive phenology of three Northern Flicker nests during 2001 at Riske Creek, British Columbia. Polyandrous female RAGG attended two nests at Nest A and Nest B and paired with two males. Her second nest, at Nest B, was the renesting attempt of the male originally from Nest C.

color banding, I should be efficient at detecting polygynous relationships, but have uncovered only this one "spontaneous" case among 352 nesting attempts monitored during four years. Two other cases involved females that abandoned their mates during incubation and renested with a neighboring male. However, these two females may have abandoned as a result of being trapped at the nest; they did not continue to attend chicks at their first nests although their first males successfully fledged a small portion of the brood alone. In contrast, female RAGG was banded in 2000 and was not retrapped in 2001 until after initiating a polyandrous relationship; therefore, human disturbance was not a proximate cause.

There are only a few reports of polyandry in other woodpeckers. Willimont et al. (1991) and Kotaka (1998) each observed one case in the West Indian Woodpecker (*Melanerpes superciliaris*) and the Great Spotted Woodpecker (*Dendrocopos major*), respectively. Wiktander et al. (2000) reported five polyandrous female Lesser Spotted Woodpeckers (*D. minor*) out of 68 breeding attempts over six years, and those were associated with a sex bias toward males in the population. Nocturnal incubation by only males within Picidae may predispose woodpeckers to polyandry, but Ligon (1999) suggested that the evolution of such a mating system was constrained because both members of a woodpecker pair were necessary during incubation and provisioning to fledge young. This may be the case generally, although in two cases at Riske Creek, male flickers that were abandoned by their mates during late incubation successfully raised young alone. The case of spontaneous polyandry I observed was advantageous for the female flicker, which fledged 13 young compared to a mean of 5.9 in the general population (n = 227 including only broods where some nestlings hatched; KLW unpubl. data). Both sexes typically feed nestlings at similar rates (Wiebe and Elchuk in press), but in this case the males apparently compensated for reduced provisioning by the polyandrous female at both nests because no nestlings starved.

A number of proximate factors may promote polyandry in woodpeckers. The skewed population sex ratio observed by Wiktander et al. (2000) was not apparent at Riske Creek, but breeding densities were high: 13 other flicker pairs nested within 1.2 km of the polyandrous group. Female RAGG was two years old according to molt criteria in Pyle et al. (1997) and her first male at Nest A was six years old. Since flickers typically mate with individuals in their own age class (KLW unpubl. data), it is unlikely that RAGG initiated a second nest with BAKG, a yearling male, because of his quality or experience. It is uncertain whether BAKG knew the reproductive status of female RAGG when he renested with her, or whether he was duped; the motivation to renest quickly may be great given the short summers at this relatively high latitude. Since home ranges of flickers overlap extensively (Elchuk and Wiebe 2002), it is almost certain the two males were aware of each other and nest sites in the area. Regardless, the timing of the two nests was staggered sufficiently so that the female could incubate at both, contributing parental care during a critical time of reproduction.

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Does Mallard Clutch Size Vary with Landscape Composition?

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ABSTRACT.—We studied Mallards (*Anas platyrhynchos*) nesting in artificial nesting structures in northeastern North Dakota and compared clutch size between landscapes where proportion of cropland was either high (mean = 68.9%, cropland landscapes) or low (mean = 30.2%, grassland landscapes). Mallard clutch size was significantly related to nest initiation date and landscape composition. Mean clutch size, controlled for nest initiation date, was 1.24 ± 0.33 SE eggs smaller on cropland landscapes than on grassland landscapes. Generality of this pattern across space, time, and type of nesting sites is unknown, as is causation. Demographic importance of variation in clutch size may be influenced by covariation with other demographic variables, such as nest success and abundance of breeding pairs, which also are negatively correlated with landscape proportion of cropland. We suggest that researchers examine relationships between clutch size and landscape composition in both structure-nesting and ground-nesting Mallards, in other geographic areas, and in other duck species. *Received 5 September 2001, accepted 3 June 2002.*

Fragmentation and destruction of habitat can influence numerous ecological processes and cause a variety of conservation problems (Zabinski and Holt 2000). Nest success of Mallards (*Anas platyrhynchos*) in the prairie pothole region declines as proportion of cropland on a landscape increases (i.e., nest success is positively correlated with landscape proportion of perennial upland nesting cover; Greenwood et al. 1995, Reynolds et al. 2001). The overall significance of this relationship could be influenced by covariation with other demographic parameters. Artmann et al. (2001) documented that the rate of occupancy of artificial nest structures by Mallards, and abundance of Mallard pairs, was lower on North Dakota sites where the proportion of cropland was high compared to where it was low. The objective of the current analysis was to determine whether Mallard clutch size also varied with landscape composition.

STUDY AREA AND METHODS

We installed 20 cylindrical artificial nesting structures on each of 13 10.4-km^2 sites during late winter, 1997, and monitored their use by Mallards during the spring of 1998. Sites were scattered over two counties (approximately 9,000 km^2) in northeastern North Dakota. The abundance and types of wetlands were similar across the study area (Artmann et al. 2001), but percent cropland differed between cropland landscapes (n = 6, mean = 68.9% cropland) and grassland landscapes (n = 7, mean = 30.2% cropland). We visited all structures 3–4 times from May through July and recorded clutch size at each visit. Mallard clutch size declines with nest initiation date (Krapu et al. 1983, Cowardin et al. 1985), so we used ANCOVA to control for initiation date and asked whether clutch size differed between cropland and grassland landscapes. The full model included landscape as a fixed factor, nest initiation date as a covariate, and their interaction. We conducted analyses using SPSS (2000), removed nonsignificant ($P > 0.05$) interactions from the final model, and assumed type III sum of squares.

RESULTS

Mallard clutch size was related to date ($F_{1,38}$ = 52.02, $P < 0.0001$) and to landscape ($F_{1,38}$ = 14.30, $P = 0.0005$). Clutch size, controlled for nest initiation date, was 1.24 ± 0.33 SE eggs smaller on cropland landscapes than on grassland landscapes (Fig. 1). Predicted mean clutch size on the mean initiation date (April 27) was 8.40 ± 0.30 SE on cropland sites and 9.64 ± 0.14 on grassland sites. Date × landscape interaction (P = 0.86) was dropped from the final model. This result suggested that the relationship of date and clutch size was similar between grassland and cropland landscapes, hence supporting the ANCOVA assumption of homogeneous slopes.

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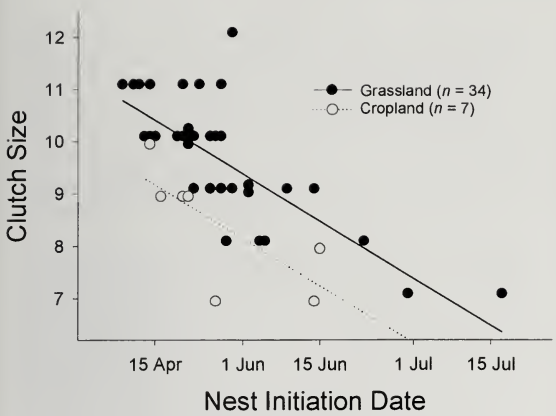

FIG. 1. The decrease in Mallard clutch size with nest initiation date differed between two landscapes, northeastern North Dakota, 1998. All nests were in artificial nest structures installed during late winter, 1997. The model for clutch size in grassland landscapes was 17.195 − 0.064date; clutch size in cropland landscapes was 15.960 − 0.064date; $r^2 = 0.63$.

DISCUSSION

Although the potential importance of variation in clutch size to Mallard demographic performance is small relative to the importance of variation in nest success (Johnson et al. 1992, Hoekman et al. 2002), nest success also declines as landscape proportion of cropland increases (Greenwood et al. 1995, Reynolds et al. 2001). Artmann et al. (2001) also found that Mallard pair abundance was substantially lower on cropland landscapes than on grassland landscapes (9.2 ± 1.0 SE breeding pairs/km^2 and 15.2 ± 1.0, respectively), and Krapu et al. (1997) noted a similar pattern. Hence, portions of the prairie pothole region with relatively large proportions of grassland remaining may represent areas where Mallard clutch size, nest success, and pair densities all are relatively high. Positive covariation of two or more demographic traits can substantially amplify their overall influence on demographic performance (van Tienderen 1995).

The observation of a substantial difference in clutch size associated with differences in landscape composition is novel in ducks, to our knowledge, but similar patterns have been documented for passerines (Dias and Blondel 1996). Furthermore, passerines may phenotypically reduce clutch size in response to high rates of nest predation (Julliard et al. 1997).

Mallard clutch size may vary with date, wetland conditions, age and nutritional condition of the female, and number of previous nesting attempts within a season (Krapu 1981, Krapu et al. 1983, Cowardin et al. 1985, Johnson et al. 1992, Rohwer 1992). Our study design allowed reasonable control for wetland conditions and date. Several potential explanations for the pattern we observed seem possible. Krapu et al. (1997) suggested that relatively high Mallard pair densities on grassland landscapes were largely a function of better feeding opportunities in untilled temporary and seasonal ponds, and clutch size is related to diet quality (Eldridge and Krapu 1988). In our study, however, wetland type and condition were similar between landscapes, and the entire area was in an exceedingly wet cycle during the study and for several years prior. Consequently, we suspect that feeding opportunities in wetlands were similar between landscapes. Relatively large clutches on grassland landscapes might simply reflect higher rates of nest parasitism where nests in structures were more common and hence more easily found (Rohwer and Freeman 1989). This potential explanation is appealingly simple, but would require that the parasitism involve only one or a few eggs per parasitized nest because we found no unusually large clutches (Fig. 1). Higher nest success (through lower nest predation) in areas with a high proportion of perennial upland nesting cover could promote increased breeding philopatry by successful females (Lokemoen et al. 1990, Anderson et al. 1992), shifting population structure toward "better" (e.g., older, fatter, more dominant) females that lay larger clutches. If larger clutches on grassland landscapes somehow reflect the presence of better females, then the question of ultimate cause and effect remains: do grassland landscapes produce better females or do better females select grassland landscapes?

Our study was limited in geographic scope to a two-county area in North Dakota, and we studied only structure-nesting Mallards. We know of no reason to expect variation in clutch size relative to landscape composition to differ between structure-nesting and ground-nesting Mallards, but gathered no data

on the latter. We suggest that researchers examine relationships of clutch size and landscape composition in other geographic areas, in both structure-nesting and ground-nesting Mallards, and in other duck species. Obtaining unbiased estimates of clutch size in ground nests likely will be difficult because partial clutch predation is common in ground nests and is difficult to distinguish from inherent variation in clutch size (Cowardin et al. 1985). We detected no evidence of nest predation in structures, so our data should be essentially free of bias from that source. If the pattern proves to be general (across years, geographic areas, and nesting habitats), an improved understanding of its magnitude and causes likely will be helpful in understanding Mallard breeding ecology, modeling patterns of recruitment, and targeting conservation efforts.

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Helping at a Henslow's Sparrow Nest in Wisconsin

Michael J. Guzy,[1,3] Christine A. Ribic,[1] and David W. Sample[2]

ABSTRACT.—We document the first reported observation of helping at the nest of a Henslow's Sparrow (*Ammodramus henslowii*). Video surveillance recorded two unbanded adults (a presumed male and female) and one banded adult male feeding chicks. No intraspecific aggression among the adults was observed. *Received 17 October 2001, accepted 28 June 2002.*

Helpers at the nest have been documented for relatively few avian species worldwide (about 3.2% of all known species; Arnold and Owens 1998), and more rarely among North American passerines (see Brown 1987). Species in which helping occurs often are sedentary with a shortage of territories, nest sites, or mates constraining independent reproduction (Brown 1987). Helpers may gain direct fitness benefits through personal reproduction, increased likelihood of territory acquisition, or increased survival, and/or indirect fitness benefits by increasing the reproduction or survival of nondescendant kin (Brown 1987, Emlen 1997, Cockburn 1998). As studies employing intensive banding efforts or close observation of nests have become more common, the incidence of helping has been detected in a growing number of migratory bird species in North America, e.g., Bobolinks (*Dolichonyx oryzivorus*; Beason and Trout 1984), Hooded Warblers (*Wilsonia citrina*; Tarof and Stutchbury 1996), Cooper's Hawks (*Accipiter cooperi*; Boal and Spalding 2000), Ovenbirds (*Seiurus aurocapillus*; King et al. 2000), and sapsuckers (*Sphyrapicus* spp.; Trombino 2000). Among the North American sparrows, helpers have been documented in only Brewer's Sparrows (*Spizella breweri*; Gill and Krannitz 1997) and Chipping Sparrows (*S. passerina*; Middleton and Prescott 1989), both of which are migratory.

Here we document an instance of helping at the nest of a Henslow's Sparrow (*Ammodramus henslowii*), a migratory grassland species in which the female performs most or all of the incubation and brooding of eggs and chicks, while the male participates in feeding the young (Rising 1996). This nest was located in southwestern Dane County, Wisconsin (42° 53′ N, 89° 44′ W). We banded Henslow's Sparrows with USFWS aluminum bands and a unique combination of three plastic color bands. We monitored the nest that is the subject of this paper by using a video camera located approximately 50 cm above the nest with a view into the nest cup, the rim of which was approximately 10 cm above the ground. Infrared lights allowed 24-h recording of activity at the nest, and tapes were changed approximately every 24 h. The nest was located in habitat dominated by smooth brome (*Bromus inermis*) and was built in a clump of standing dead grass from the previous season's growth. In reviewing the tapes we were able to determine that three different birds, all with adult plumage, participated in feeding the chicks.

Before the eggs hatched, the presumed female was the only bird recorded at the nest cup. This bird was unbanded but had an irregular crown stripe that allowed it to be visually distinguished from other birds at the nest, and was the only bird we observed incubating eggs or brooding chicks. After the eggs hatched (approximately 06:00 CST on 17 July 2001), she periodically left the nest for intervals of a few seconds to 20 min, returning with a food item each time. During this time the female was the only bird we observed at the nest. Storms caused the camera lens to be obscured at approximately 3.5 h after hatching, blocking direct observation of the nest cup. On day 2 at 10:42 (approximately 28 h after hatching) direct observation of the nest cup was restored. At this time the presumed female remained at the nest

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while a different, unbanded individual brought food items to the nest cup and either transferred them to the female at the nest or fed the chicks directly, but never attempted to brood the chicks. We presumed this bird to be a male based on behavioral observations of a known male (see below) which behaved in a similar manner. The female often left the nest 1–2 s before the arrival of the male bird. The female returned 2–18 min later with a food item; if another bird was present, it usually left the nest as the female returned. During this period (10: 42–19:52), we saw only unbanded birds at the nest. On day 3 we observed the female at the nest when a banded male brought an insect. This bird's identity was determined based on a unique color band combination and its gender by the presence of a cloacal protuberance (detected when we banded the bird). This bird had been banded 16 July 2001, the morning before the eggs hatched, ≤200 m from the nest. On day 3, during 9 h 16 min of feeding activity, the unbanded male visited 23 times and the banded male visited 35 times. We recorded all three birds removing fecal sacs, and none of the adults exhibited intraspecific aggression. This nest was depredated on day 3, 79 h after hatching, ending the activity at the nest.

Some possible explanations (see Brown 1987) of our observations include (1) polyandry, (2) an offspring or sibling of one or both parents from a previous year feeding chicks, or (3) an unrelated adult "adopting" the chicks and joining the breeding pair in care of the chicks. Polyandry cannot be confirmed or dismissed. Behavioral clues to the mating system are missing because observation of the adults was restricted to the view of the camera and began late in the nesting cycle. Given the low incidence of polyandry in birds (Brown 1987), while possible, this seems an unlikely explanation.

Siblings helping to raise siblings, or siblings of one of the breeders helping to raise the breeder's offspring are not uncommon among cooperative breeders (see Brown 1987, Stacey and Koenig 1990). However, an offspring of one or both parents from the previous year (or one of the breeder's siblings) appears unlikely given that return rates of juvenile migrant passerines to the natal area typically are very low (Weatherhead and Forbes 1994). Return rates of adult Henslow's Sparrows, albeit based on relatively few banded birds, appear to be very low as well (≤17%, Burhans 2001; 1 of 41 in the present study area, MJG unpupl. data). All three birds we observed were in adult plumage, indicating they were ≥1 year old (Pyle et al. 1997), and thus could not have been from a clutch earlier in the season.

In many species, adults have been observed feeding chicks of their own species or other species in nearby nests, sometimes in addition to attending their own nest (see Shy 1982 for review), but this has not been reported for Henslow's Sparrows. In some instances, inter- and intraspecific feeding occurs when an adult has lost its own clutch and it adopts a nearby nest temporarily or permanently. This seems the most likely explanation for the observed behavior in the absence of other data. Overall, nest failure in the study area was high (approximately 75% of grassland bird nests failed), with predation being the main cause for failure. Also, the banded bird was not observed at the nest until ≥3 days after it was banded; however, it could have been transferring food to the female out of view of the camera.

As no population of Henslow's Sparrows have been studied sufficiently well enough to know the frequency of helping, more study is needed. As a species that has undergone population declines throughout its range, information on the frequency of helping or polyandry may be critical in designing monitoring schemes to accurately gauge future population changes. In the presence of helping or polyandry, any monitoring scheme based on singing males and that assumes each male represents a breeding pair could potentially overestimate the number of breeding females and thus the effective population size.

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Adoption of Black-winged Stilt Chicks by Common Terns

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ABSTRACT.—We report an instance of interspecific adoption of Black-winged Stilt (*Himantopus himantopus*) chicks by Common Terns (*Sterna hirundo*), two species that nest in similar habitats but differ substantially in their behavior and diets. This is the first report of adoption between these two species. *Received 2 November 2001, accepted 30 June 2002.*

Adoption has been defined as care given to young or eggs by unrelated adults. This can happen when alloparenting occurs instead of breeding (Riedman 1982, Dukstra et al. 1997) or as a result of misdirected parental behavior (Čapek et al. 2000). Intraspecific adoption has been reported in many species, e.g., Herring Gulls (*Larus argentatus*; Holly 1981), Red-throated Bee-eaters (*Merops bulocki*; Fry 1972), Peregrine Falcons (*Falco peregrinus*), Northern Goshawks (*Accipiter gentilis*), Yellow-bellied Sapsuckers (*Sphyrapicus varius*), Black-capped Chickadees (*Poecile atricapillus*), Prairie Warblers (*Dendroica discolor*; Rohwer 1986), South Polar Skuas (*Catharacta maccormicki*; Skutch 1987), European Starlings (*Sturnus vulgaris*; Smith et al. 1996), and Eurasian Blackbirds (*Turdus merula*; Dukstra et al. 1997).

Interspecific adoption is much less common. Song Sparrows (*Melospiza melodia*) have adopted Yellow Warbler (*Dendroica petechia*) chicks (Lozano and Lemon 1998) and Blackcaps (*Sylvia atricapilla*) have adopted Yellowhammer (*Emberiza citrinella*) chicks

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(Čapek et al. 2000). In the cases that have been reported there were only minor differences in the behavior and diet of the adopting and adopted species. Midura et al. (1991) reported a case in which a Least Tern (*Sterna antillarum*) adopted a nest with three Piping Plover (*Charadrius melodus*) eggs. The tern laid two more eggs and incubated all five. After the eggs hatched, the observers transferred the only surviving Piping Plover chick to another family of Piping Plovers, so no further interactions were observed.

Skutch (1987) reported on adoption in passerines, including Winter Wrens (*Troglodytes troglodytes*) that adopted Great Tit (*Parus major*) chicks, Carolina Wrens (*Thryothorus ludovicianus*) that adopted Great Crested Flycatcher (*Myiarchus crinitus*) chicks, Scarlet Tanagers (*Piranga olivacea*) that adopted Chipping Sparrow (*Spizella passerina*) chicks, and Song Sparrows that adopted American Robin (*Turdus migratorius*) chicks. These chicks were observed being fed by breeding males while the females were still incubating; the unrelated chicks were neglected as soon as the host chicks hatched. Here we report an unusual case of adoption between two species with very different morphological, behavioral, and nutritional characteristics.

A colony of Common Terns (*Sterna hirundo*) has existed since at least 1970 on a 350-m^2 flattened sandbank situated in about 100 ha of salt ponds in Atlit on the Mediterranean coast, about 12 km south of Haifa (32° 42′ N 34° 59′ E). About 30 m from the sandbank there is an embankment, where vehicles, people, and dogs cause intermittent disturbance. During the early 1970s five pairs of Little Terns (*S. albifrons*) joined the colony and their number increased rapidly. During early June, 2001, there were about 300 pairs of each species on the sandbank. Most (about 200 pairs of each species) had chicks on the day of the observation. Also in the vicinity were about 40 pairs of Black-winged Stilts (*Himantopus himantopus*). Whereas the two species of terns nest mainly on the sandbank, and sometimes on artificial embankments between the ponds, the stilts usually build their own nests in shallow water, but occasionally nest on the embankments or on small islands with halophytic vegetation. The stilts make small, truncated, cone-like nests of gravel and earth, and these nests persist in the ponds for several years. Terns commonly use abandoned stilt nests, perhaps because of crowding on the sandbank. We also have observed terns aggressively trying to evict other terns, stilts, and even Avocets (*Recurvirosta avosetta*) from their nests, often with success.

On 8 June 2001, about 50 m from the main area of the tern colony, near a nest where we had observed Black-winged Stilts incubating a few days earlier, three one-day-old stilt chicks were walking around. While we watched the chicks, the entire colony of terns flew up, a typical response to an actual or perceived threat from predators or humans (Gochfeld and Burger 1996). This behavior always is accompanied by alarm calls. In response to the alarm calls, all the tern chicks crouched or ran for shelter, whereas the stilt chicks continued to walk and feed along the banks of the pond. They did not exhibit the usual response to warning calls given by their parents, i.e., squatting motionless or running for shelter (Cramp and Simmons 1982). We did not hear stilt alarm calls over the vociferous flock of terns nor did we see any stilts among them. Black-winged Stilt chicks fledge at 28–32 days of age, and the adults typically continue to attend them for another 2–4 weeks, but sometimes the family stays together for several months (Pierce 1996).

After a minute or two a pair of Common Terns landed on the old stilt nest, near the chicks that walked around it. Terns usually are very aggressive toward intruders in their nesting territory and may even kill neighbors' chicks (Gochfeld and Burger 1996), but in this case they showed no signs of aggression toward the stilt chicks. After a short time the chicks approached the terns and stood in the shade beneath them. A few minutes later, one of the terns attempted, unsuccessfully, to feed a small fish to one of the stilt chicks. At twilight, the three stilt chicks gathered around the terns and crouched beneath them, evidently for warmth and shelter during the night.

This unusual behavior motivated us to observe the phenomenon intensively during the following 10 days. The terns tried repeatedly to feed the stilt chicks with small fish, but the chicks ignored them. Instead, the chicks walked around the nesting site and fed by

themselves on insects, mollusks, crustaceans, and other aquatic invertebrates. We observed one of them capture a fly. Occasionally on hot days, the chicks returned to the nest site and rested in the shade beneath the adoptive adult terns. Toward evening they regularly returned to the nest and crouched beneath the belly of the tern through the night.

The terns protected the chicks from Little Egrets (*Egretta garzetta*) and Egyptian Mongooses (*Herpestes ichneumon*); when these potential predators approached the chicks, the terns wheeled above them, uttering alarm calls, swooped upon them, and even attacked them with their bills. The terns even drove off a neighboring male stilt that may have been the biological father of the chicks. During the first five days the chicks appeared to develop normally, but as their legs grew longer it became increasingly difficult to crouch under the terns. After six days, the smallest chick, which apparently had a diseased or injured leg, disappeared. Two days later, we found another chick dead in the nest. The last stilt chick survived until 10 days of age and then died in the nest during the night. The long-legged stilt chicks had no longer been able to crouch under the adult terns, even when the terns lifted themselves in an apparent attempt to accommodate the chicks. Consequently, we assume that the last two died from exposure.

There are many differences between the behavior of Black-winged Stilt and Common Tern chicks. The tern chicks remain in the nest for about four days after hatching, after which they seek refuge in vegetation within the nesting territory and emerge mainly when they hear a parent approaching. They usually do not venture farther than a few meters from the nest until the fledging stage. During this period they do not forage by themselves, but instead depend upon being fed small fish by their parents (Cramp 1985, Gochfeld and Burger 1996, Paz 1986). In contrast, within 24 h of hatching, the adult stilts normally lead their chicks away from their nest to a feeding area, sometimes hundreds of meters away. While leaving the nesting site the chicks walk along the banks and even swim in the water (Cramp and Simmons 1982, Pierce 1996; UP unpubl. data). In both species there is vocal communication between the parents and the chicks, but their calls are quite different and, except for the alarm calls, serve different purposes. Adult stilt calls attract the chicks to follow their parents to the feedings grounds (Pierce 1996), while adult tern calls serve mainly to announce the arrival of the parents with fish. A behavioral characteristic in chick rearing common to the two species is that parents provide warmth and shelter during the night and sometimes shade during the day.

We speculate that during incubation, the stilts abandoned the nest or were killed. Alternatively, the aggressive terns may have evicted the stilts because of limited availability of suitable nesting sites in the main colony, as suggested by Riedman (1982) and Midura et al. (1991). The terns then occupied the nest with the stilt eggs and began to incubate them. They apparently could not distinguish between their own and stilt eggs because the eggs are very similar both in size and color. In addition, both species regularly have three eggs in a clutch. These similarities may have led to misdirected parental behavior (Čapek et al. 2000).

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Nectarivorous Feeding by Shiny Cowbirds: a Complex Feeding Innovation

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ABSTRACT.—Here I report a feeding innovation by Shiny Cowbirds (*Molothrus bonariensis*) in which the birds feed on the nectar of flax (*Phormium tenax*) flowers. Flax frequently is cultivated in Mar del Plata City, Buenos Aires Province, Argentina, as an ornamental plant, and the Shiny Cowbird is common there. The length of the cowbird's bill is similar to that of the flax flower tube, which permits the cowbird to access the nectar. Further, the panicle stem of the flax is sufficiently rigid for perching, and the short distance between the stem and the flower enables a perched cowbird to reach the flower. At this site, flax nectar probably is utilized in a sustainable manner, as the flowers apparently are not harmed. Future investigations should examine whether or not the observed behavior is restricted to this particular population and if it is not, determine the spatial and temporal extent to which it occurs. *Received 12 October 2001, accepted 5 September 2002.*

Organisms possessing socially modulated behavioral flexibility may improve their fitness under some circumstances (Bonner 1980). For example, these organisms may identify new foods and food sources, acquire new feeding techniques, increase their exploration and foraging efficiency, and recognize predators and poisonous foods. Many feeding innovations have been reported for birds (Lefebvre et al. 1997). One notable example was the opening of milk bottles by Great Tits (*Parus major*; Fisher and Hinde 1949). Here I report on a feeding innovation by Shiny Cowbirds (*Molothrus bonariensis*) in which the birds feed on nectar from flax flowers (*Phormium tenax*). There are no previously published observations of this feeding behavior in Shiny Cowbirds. However, Morton (1979) recorded three other icterids feeding on nectar, Yellow-backed Orioles (*Icterus chrysater*), Orchard Orioles (*I. spurius*), and Baltimore Orioles (*I. galbula*).

During the 20th Century, the geographic distribution of the Shiny Cowbird increased extensively from its original distribution in southeastern South America. The species currently ranges west to Chile (Marín 2000), and north to the Caribbean islands (Cruz et al. 1985) and (since 1985) Florida in the United States (Lowther and Post 1999). This species benefitted from human-modified environments during the last century by using urban areas and open habitats with dispersed trees (Cruz et al. 1985, Ridgely and Tudor 1989, Canevari

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et al. 1991). The Shiny Cowbird is an extreme generalist in both its breeding and feeding behavior. Shiny Cowbirds are brood parasites, parasitizing >200 host species (Friedmann and Kiff 1985), and feed omnivorously, mainly on seeds and arthropods (Camperi 1984, Canevari et al. 1991). The flexibility displayed by Shiny Cowbirds in both its host generalist strategy and omnivorous diet may be responsible for their range expansion, as such generalist behavior enables them to exploit novel, modified habitats and food sources.

The Shiny Cowbird is a common bird of the urban avifauna of Mar del Plata City, Buenos Aires Province, Argentina (38° 00′ S, 57° 34′ W). Since my first record in 1991 (JPI unpubl. data), I occasionally have observed cowbirds feeding on nectar from flax flowers along the Playa Grande coast of Mar del Plata City. Beginning with the austral spring 1998 through the austral summer 2001, I observed four flax plants on an almost daily basis. From November to January of each year, 1–3 cowbirds fed on nectar, mainly during morning and afternoon. I did not observe cowbirds feeding on nectar from flowers other than flax.

Flax is a rhizomatous plant native to New Zealand (Dimitri 1978). It frequently is cultivated in Mar del Plata City as an ornamental plant. During spring, large leafless stems grow panicles, each containing approximately 400 flowers. Plants have 15–20 panicles, with a total of 6,000–8,000 flowers per plant.

When feeding, the Shiny Cowbird perches on the large stem of the flax panicle and inserts its bill and forehead into the flower tube. Contact with the flowers results in the cowbird's forehead turning orange with pollen. This feeding behavior is facilitated by the flax panicle stem being rigid enough for perching, and by the short distance between the stem and the flower, which allows the cowbird to reach the flower. I measured the bill of a cowbird and 20 flax flowers to assess if the size of the flower constrained access to the nectar by cowbirds. The measurements of the beak and skull of one male cowbird from the collection of Vertebrate Lab, Faculty of Natural Sciences, Mar del Plata Univ., Argentina, were: culmen 16.8 mm, basal bill height 8.7 mm, basal bill width 10 mm, and culmen and forehead 21.5 mm. The flax flower is tubular; mean measurements of the tubes were: length 26 mm, basal diameter 7 mm, and diameter at opening 9 mm. The measurements of the flax flower tube and cowbird bill are similar, reducing the possibility that size differences constrain the cowbird's access to flax nectar.

I also observed two hummingbird species, the White-throated Hummingbird (*Leucochloris albicollis*) and the Glittering-bellied Emerald (*Chlorostilbon aureoventris*), occasionally feed on the nectar of flax flowers, but with a much lower frequency than that observed for cowbirds. I observed no other bird or insect feeding on flax nectar. Shiny Cowbirds are not known to parasitize nectarivorous species in Mar del Plata, so the possibility that this behavior was learned from hosts is unlikely.

During the Miocene, the rapid diversification of flowering plants and insects opened new niches for nectar-feeding birds, resulting in an explosive radiation of birds (Regal 1977). Nectarivorous birds are abundant in many parts of the world and include some of the largest families, such as Meliphagidae in Australia, Nectriinidae and Promeropidae in Africa, and Trochilidae in northern and Neotropical America (Collins et al. 1990). Nectarivory also has arisen in a few species within some otherwise non-nectarivorous families, such as Psittacines in Asia and Oceania (Collar 1997). In each of these cases, species have evolved morphological adaptations to feed on nectar, including changes in bill shape, tongues, and digestive systems, or other adaptations associated with strategies to access flowers (e.g., hovering in hummingbirds; Gill 1994).

To fulfill dietary requirements or to compensate for decreased nectar availability, nectarivorous birds occasionally eat other items such as insects, fruits, and seeds. However, examples of non-nectarivores exploiting nectar are rare, probably because nectarivory is a complex feeding behavior that includes important morphological constrains restricting flower and nectar access. Some insectivorous Old World warbler species (*Sylvia* spp.) exhibit nectarivorous habits after long distance flights during spring migration (Schwilch et al. 2001). Neotropical migrants and nonmigratory species also exhibit nectar feeding in the Panama Canal Zone. These include the Tennessee Warbler (*Vermivora peregrina*), Orange-chinned Parakeet (*Brotogeris jugularis*), White-necked Jacobin (*Florisuga melli-*

vora), Red-crowned Woodpecker (*Melanerpes rubricapillus*), Lesser Antillean Saltator (*Saltator albicollis*), tanagers (*Thraupis* spp. and Crimson-backed Tanager, *Ramphocelus dimidiatus*), and orioles (*Icterus* spp.; Morton 1979, 1980).

Cowbird nectarivory apparently does not harm the flax flower; thus, cowbirds are using the resource in a sustainable manner. This possibility is supported by verification that cowbirds can return at least twice to the same flower at different times (JPI pers. obs.). This sustainability contrasts with granivory and insectivory, both of which are extractive. In the U.S., there have been reports of Northern Cardinals (*Cardinalis cardinalis*) feeding on nectar; however, they nip off and eat nectar-filled flower capsules (Wible 1974). Such destructive behavior is not typical of nectarivorous species that only probe the flower.

Flax was introduced to the region approximately 50 years ago. During the past ten years, cowbirds do not seem to have extended this habit to other localities where flax is common (JPI pers. obs.). Nevertheless, considering that cowbirds are expanding their geographic distribution by colonizing new habitats (Cruz et al. 1985, Lowther and Post 1999, Marín 2000) nectarivory by cowbirds may be expected to spread to other localities (e.g., Lefebvre 1995) by cultural transmission. Thus, future observations should determine if nectarivory is restricted to this population, and if it is not, determine the spatial and temporal distribution in which nectarivory occurs.

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Re-evaluating the Bay-breasted Warbler Breeding Range: Nine Years of Presence in Lower Michigan

Kevin Ellison,[1,4,5] Paul W. Sykes, Jr.,[2] and Carol I. Bocetti[3]

ABSTRACT.—The breeding range of the Bay-breasted Warbler (*Dendroica castanea*) is thought to include only the northernmost portions of six northeastern and northcentral states in the United States. During a 10-year banding study of Kirtland's Warblers (*Dendroica kirtlandii*) in northern Lower Michigan, we caught 44 Bay-breasted Warblers outside of their reported migration dates during 9 of the 10 years. Two birds captured in 1997 were in breeding condition; one possessed a cloacal protuberance and the other a full brood patch. We also captured two hatching year birds with fleshy rictal flanges in 1997. We suggest that these records indicate a long term presence of Bay-breasted Warblers on breeding grounds considerably farther south than previously recorded. *Received 6 November 2001, accepted 15 August 2002.*

The breeding range of the Bay-breasted Warbler (*Dendroica castanea*) is restricted to coniferous forests of northeastern and northcentral North America (Sealy 1979). Breeding has been documented within the Upper Peninsula of Michigan and areas of five other northern states, which constitute the portion of the warblers' breeding range within the United States (Brewer et al. 1991, Williams 1996, Dunn and Garrett 1997). This species exhibits extensive vagrancy in response to caterpillar outbreaks outside its typical habitat and range (Sealy 1979, Patten and Burger 1998). However, vagrant Bay-breasted Warblers rarely have been recorded during the breeding season (see Sealy 1979). Here we report data from 10 years of mist netting to document Bay-breasted Warbler presence outside of its normal migration dates in the Lower Peninsula of Michigan.

FIG. 1. Bay-breasted Warblers were captured prior to migration in northern Lower Michigan, 1986–1997 (excluding 1993–1994). Number of captures per county were (1) 8 adults and 2 hatching year birds in Crawford County; (2) 17 adults, including 1 with a cloacal protuberance, in Oscoda County; (3) 7 adults, including 1 with a brood patch, in Alcona County; (4) 1 adult in Roscommon County; (5) 3 adults in Ogemaw County; and (6) 6 adults in Iosco County.

During a 10-year banding project in jackpine (*Pinus banksiana*) forests of northern Lower Michigan (Fig. 1), we captured 226 Bay-breasted Warblers between 16 May and 22 September, 1986–1997 (excluding 1993–1994). The long term banding project was designed to measure seasonal productivity, movements, and dispersal of the endangered Kirtland's Warbler (*D. kirtlandii*), so we conducted mist netting outside the Kirtland's Warbler nesting season. However, we captured 44 Bay-breasted Warblers before 5 August, which is prior to the passage of migrants (hatching year Bay-breasted Warblers, which migrate before adults, pass through the region during late August; Dunn and Garrett 1997).

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Fall migration dates ranged between 16 August and 30 September, 1979–1995, in southeastern Michigan (J. A. Creaves unpubl. data cited in Williams 1996), southeastern Minnesota (Winker et al. 1992), and southern Maine (Morris et al. 1994). Moreover, two Bay-breasted Warblers captured in 1997 at different locations were in breeding condition. One male with a full cloacal protuberance (*sensu* Pyle et al. 1997) and one female with a full brood patch were caught 18 July and 5 August, respectively. Also, we captured two hatching year Bay-breasted Warblers on 23 July 1997; each was in prebasic I plumage (Williams 1996) with fleshy rictal flanges. This direct evidence of breeding, and the 44 captures through 5 August, supports our conclusion that Bay-breasted Warblers regularly breed on the Lower Peninsula of Michigan. By the 5 August criterion, we suggest Bay-breasted Warblers breed as far south as Iosco, Ogemaw, and Roscommon counties (Fig. 1). Thus, breeding likely occurred in these counties during 9 of the 10 years represented by our capture data. Such breeding may have occurred in the past and gone undetected due to this warbler's high-pitched song (Dunn and Garrett 1997). Furthermore, the potential for detection has been limited by restricted public access to northern Lower Michigan conifer stands since the early 1970s to protect breeding Kirtland's Warblers.

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Ornithological Literature

Edited by Sara R. Morris

WILDLIFE OF THE GALAPAGOS. By Julian Fitter, Daniel Fitter, and David Hosking. Line illustrations by Martin B. Withers. Princeton Univ. Press, Princeton, New Jersey. 2000: 254 pp., numerous color photographs and line drawings. $19.95 (paperback).—The *Wildlife of the Galapagos* is somewhat of a misnomer for this pocket reference and field guide. This small tome includes identification and natural history information on the birds, reptiles, aquatic mammals, land mammals, invertebrates, and plants. An introductory section provides a key to species status, which includes information about whether a species or subspecies is endemic, native, or introduced, and the residency status of a species ranging from resident to migrant to occasionally observed. Numerous photographs illustrate the species and habitats of the islands. For the common species in the Galapagos, the authors include a list of locations where the species is best viewed.

For the distinctive species of the islands, the authors include additional information that may be of interest. For example, in the section on the Blue-footed Booby (*Sula nebouxii*), the authors include a description of the elaborate mating ritual of the species. When covering the Galapagos finches, the authors include a description of Darwin's voyage, a discussion of the importance of these species in the theory of evolution, and as an example of adaptive radiation, a tree showing the different lines of evolution within the group. Unlike most other species, the finch descriptions are accompanied by range maps for each species. The section on the Galapagos Tortoise (*Geochelone elephantophus*) is particularly well done. In addition to providing substantial details about the life history of the tortoises, there is considerable information about each of the subspecies, including the island or caldera where each is found, the shape of the carapace (including photographs and diagrams), and the population size and conservation concerns. Another example of how this is much more than a field guide is found in the narrative about the Galapagos Green Turtle (*Chelonia mydas agassisi*), where the authors include information on temperature-dependent sex determination in this species.

Following the species accounts, the authors cover the basic geology and volcanology, the history, ocean currents and climate, and more on the conservation of the islands. The geology section includes a discussion of the Galapagos hot spot, plate movements, and descriptions and photographs of a number of geological features. The history is brief, but provides a context for the human habitation of the islands. Many visitors will find the section on ocean currents to be of particular interest in explaining the unexpected cold temperature of equatorial waters.

One of the most useful portions of the book for visitors to the islands is a section on visitors' sites. For each of the commonly visited landings among the islands, there is a map that includes the trails, possible swimming areas, and indicates if there is a wet landing; a list of the species of plants and animals that are likely to be encountered; and a description of the background of the site. The lack of a key to the symbols is a little difficult, particularly for those not already familiar with the areas, but nonetheless, the inclusion of this resource is excellent.

Additional sections provide an extensive introduction to the islands for visitors to this unique area. Following the introduction is a map of the islands and a list of all the islands that includes their Spanish name, English name, and the derivation of both names, if known. The national park rules are enumerated, with additional reasons or explanations of many of the rules. An additional section on field photography includes information about equipment, covering such topics as camera choices (including a comparison of SLR and digital equipment), lens choices, film, and accessories, and photographic techniques, including lighting, exposure, depth of field, shutter speed, composition, and a code of conduct. A one-page conservation plea from the

director of the Galapagos National Park and the director of the Charles Darwin Research Station provides visitors with a mechanism to contribute to the preservation of the islands. A bibliography of additional references and a glossary of terms will greatly help the more enthusiastic visitor.

Because of its size, this guide is not as comprehensive as individual taxon specific guides. There are a number of minor changes that could make the volume more useful. For example, in the birds section, many of the identifying features which are described in the text are not shown in the accompanying photographs. Although there often is a list of locations where particular species can be viewed, the lack of range maps will be frustrating to the more serious natural history enthusiast. Anyone familiar with the taxonomic arrangement of birds will find the organization of the birds as seabirds, coastal birds, and landbirds to be somewhat frustrating.

Although not as comprehensive as individual guides for the flora, fauna, or geology of the islands, this field guide should be strongly considered by anyone looking for a single broad field guide reference during a trip to the Galapagos Islands. I showed this book to several students I took to the Galapagos, and they all wished that it had been available for their trip. Although it is basic in many areas, the *Wildlife of the Galapagos* provides a nice introduction to the islands and should be strongly considered by anyone looking for a single reference for an initiation to the islands or to keep their luggage lighter for their other equipment.—SARA R. MORRIS.

THE BIRDS OF ECUADOR, VOLUME I: STATUS, DISTRIBUTION, AND TAXONOMY. By Robert S. Ridgely and Paul J. Greenfield. Cornell Univ. Press, Ithaca, New York. 2001: 848 pp. $60 (paperback), and BIRDS OF ECUADOR, VOLUME II: FIELD GUIDE. By Robert S. Ridgely and Paul J. Greenfield. Cornell Univ. Press, Ithaca, New York. 2001: 740 pp., 96 color plates, numerous black and white maps. $50 (paperback).—The two-volume *Birds of Ecuador* set is a long-awaited addition to the guides available for birders in South America. In recognition of the scope and volume of this work, the authors chose to divide the work into two volumes, one which can serve as a reference that is not taken into the field and a second designed as the field guide.

As its name suggests, *Volume I* is an extensive volume that covers the status, distribution, and taxonomy of Ecuadorian birds. The introductory material begins with an extensive "Plan of the Book," which includes information on the layout of the two volumes and details the authors' choices in taxonomy, names, area covered in the volume, abundance designation, species accounts, and references. This section also includes a list of species that are considered hypothetical, which the authors describe as lacking hard evidence of their occurrence in Ecuador, and a list of recent species, which covers the species that have been documented in Ecuador during the last few decades. A map of Ecuador is followed by a description of the geographic regions, the climate, and the major habitat types. The section, "Bird Migration in Ecuador," covers boreal (Nearctic-Neotropical), austral, and intratropical migrants as well as pelagic visitors, birds that disperse from Peru, and wanderers. "Ecuadorian Ornithology" includes information about the ornithological activity in Ecuador since the 1920s, when the last review was published, and is followed by "A Gazetteer" that provides an introduction to the regularly mentioned localities that provide much of the distribution data in the text. "Endemic Bird Areas in Ecuador" describes nine areas that are endemic centers and provides a list of the endemic species to those areas. A section on conservation covers many of the country's conservation concerns, including "Land Protection," "Conservation Status of At-Risk Bird Species," and a list of conservation considerations, which provides some context for the conservation problems that ends in what the authors describe as a call to arms.

Individual species accounts are arranged by order and family. Prior to the species accounts within a family, there is a brief introduction to the family that includes the number of genera and species found in Ecuador, information about the worldwide distribution of the family, and may include other information perti-

nent to the family, such as information about the systematics or distribution of the family. In the individual species accounts, the authors include common name in English, common name in Spanish, and scientific name; the abundance, habitats, and movements of the species; synonyms or other common names for the species; information about different races; and range information. The taxonomy generally follows the 1998 AOU checklist. These sections often include references both of published accounts and unpublished records of many of the ornithologists working in Ecuador.

Volume II is the field guide of the set. The species accounts in the *Field guide* include the species' English, Spanish, and scientific names; species descriptions; how to tell the species from each other; information on the species' habits and voice; and a distribution map that included elevation. The book includes color plates illustrating most of the species in Ecuador, with facing pages that include important identification characteristics. These illustrations often include images of both males and females and occasionally juveniles.

My criticisms of this work are relatively minor. Even though it is only half of the whole work, the *Field guide* is extensive and will be more than many biologists will want to carry regularly in the field. Furthermore, as a visitor to Ecuador, I was disappointed by the authors' decision not to cover the avifauna of the Galapagos Islands in an already extensive work. The absence of these species means that anyone visiting both the Galapagos and mainland Ecuador will need to carry two separate field guides.

This extensive work represents substantial effort and is unquestionably the best resource available for the avifauna of Ecuador. This two-volume set is a must for anyone interested in Ecuador's birds.—SARA R. MORRIS.

FIELD GUIDE TO THE WILDLIFE OF COSTA RICA. By Carrol L. Henderson. Illustrations by Steve Adams. Univ. of Texas Press, Austin. 2002: 539 pp., numerous color photographs and line drawings. $39.95 (paperback).—The *Field guide to the wildlife of Costa Rica* is a beautifully illustrated reference to the fauna of Costa Rica. The introduction includes sections on "Historical Perspective," "Geography," "Biogeography," "Endemic Species," "Major Biological Zones," and "Wildlife Overview and Species Coverage." The introductory material is extensive, and goes beyond the scope of a general field guide. For example, the history section includes information about a number of individuals and organizations that have been instrumental in Costa Rican research, the establishment of educational organizations in tropical biology, the preservation of Costa Rican forests and wildlife, and the importance of nature tourism. The section on major biological zones includes a diagram of where each zone is found, illustrative photographs of the habitat, and a description of the habitat types and locations. The author also includes information about how elevation affects species diversity and climate and a description of each of the elevational zones.

The fauna of Costa Rica is divided into the following groupings: "Butterflies and Moths," "Other Invertebrates," "Amphibians," "Reptiles," "Birds," and "Mammals." Within each species account is the common, scientific, and Costa Rican names where available; the size and description of the species; the geographic and elevational ranges; a description of the organisms and some information on its natural history; and a location map. For the reptiles, birds, and mammals, the author also includes information on his own sightings of the species during his trips to Costa Rica. The species described also are illustrated by stunning photographs. The author recognizes that he covers only a fraction of all the species found in Costa Rica. For example, he covers only 24 species of butterflies and moths, which represents only a very small percentage of the more than 9,000 Costa Rican species.

An extensive glossary will be useful to readers who are not familiar with many of the biological and local terms used in the text. After the glossary, the author includes several appendices, which cover conservation organizations and field stations, sites included in distribution maps, wildlife vocalization resources, and a checklist for a Costa Rican trip.

Like many books called field guides, this volume is unlikely to be effective as a field guide. It is too large to be comfortably carried in the field. Had the author truly wanted the book to be a field guide, he could have used lighter paper, decreased the coverage in the introduction and the amount of white space, and decreased the extent of the text. However, it is a beautiful reference for a variety of Costa Rica's animals and may provide a nice addition to the library of biologists and natural history enthusiasts interested in Central America in general, and Costa Rica in particular.—SARA R. MORRIS.

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A NEW SPECIES OF FOREST-FALCON (FALCONIDAE: *MICRASTUR*) FROM SOUTHEASTERN AMAZONIA AND THE ATLANTIC RAINFORESTS OF BRAZIL

ANDREW WHITTAKER[1]

ABSTRACT.—I describe a new species of *Micrastur* (forest-falcon) from the rainforests of Brazil and adjacent northeastern Bolivia. Initial detection of the cryptic new taxon was enabled through hearing its distinctive voice, notably different from any of its congeners. Several specimens of the undescribed species subsequently were located in several museums; because the new species closely resembles *M. gilvicollis* (Lined Forest-Falcon), these specimens had remained unrecognized for more than a century. The new taxon not only has a vocal repertoire that differs from those of congeners, *M. gilvicollis*, *M. plumbeous* (Plumbeous Forest-Falcon), and *M. ruficollis* (Barred Forest-Falcon), but it also exhibits subtle yet consistent morphological distinctions that distinguish it from all other forest-falcons. This elusive raptor inhabits humid *terra firme* forest in southeastern Amazonia, and a disjunct population exists in the Atlantic rainforests of eastern Brazil (the latter known only from historic specimens) and merits great conservation concern. I summarize current information on the new species' distribution, offer insight into its natural history and conservation, and discuss its systematic relationships within the genus *Micrastur*. *Received 19 November 2001, accepted 30 September 2002.*

RESUMO.—Eu descrevo uma nova espécie de Micrastur (gavião florestal) da floresta tropical do Brasil e adjacente nordeste da Bolívia. O descobrimento inicial do novo cryptico táxon foi capacitada pela sua distinta voz, notavelmente diferente de qualquer um dos congêneres. Vários espécimes das espécies não descritas foram subseqüentemente localizadas em vários museus; devido à nova espécie assemelhar-se do *M. gilvicollis* (falcão-mateiro), estas espécimes ficaram desconhecidas por mais de um século. O novo táxon não somente tem um repertório vocal que difere desses congêneres, *M. gilvicollis*, *M. plumbeous*, (falcão-chumbo) e *M. ruficollis* (falcão-caburé), mas isto ainda também sutilmente exibe uma distinção morfológica que o distingue de todos os outros *Micrastur*. Este gavião evasivo habita nas matas de *terra firme* úmida do sudeste da Amazônia, e com uma população disjunta existindo na mata Atlântica do leste do Brasil (o ultimo conhecimento somente através de espécimes históricas) e merece grande interesse de conservação. Eu sumariei informações atuais sobre a distribuição da nova espécie, e presenteei a introspecção dentro da história natural e conservação, e discuto o seu relacionamento sistemático dentro do gênero *Micrastur*.

At dawn on 28 October 1997, while in lowland *terra firme* forest at Caxiuanã, Pará, Brazil, I tape recorded an unfamiliar bird vocalization that I suspected belonged to some species of forest-falcon (*Micrastur* spp.). I employed tape playback in an attempt to locate the bird. After about 10 min a forest-falcon responded vocally and then approached, land-

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FRONTISPIECE. *Micrastur mintoni* sp. nov., Cryptic Forest-Falcon, a new species of raptor from tropical rainforests of southeastern Amazonian Brazil, extreme eastern Bolivia, and the Atlantic rainforests of eastern Brazil. Adult female (holotype) is above subadult male. Figure is from a mixed media oil painting by P. J. Greenfield.

ing close by in the midstory. This unfamiliar-sounding bird looked almost exactly like *M. gilvicollis* (Lined Forest-Falcon), a species with which I had extensive field experience. I noted a few subtle but distinctive plumage differences from *M. gilvicollis*, and thus suspected that that the bird I was observing represented a cryptic *Micrastur* species previously undescribed.

Upon subsequently examining specimens of *M. gilvicollis* at the Museu Paraense Emílio Goeldi (hereafter MPEG) in Belém, Brazil, I found the specimens could be sorted into two distinctly different plumage types. Twenty-three specimens matched the field characters of the bird I observed in Caxiuanã and 12 fitted *M. gilvicollis*. I, together with MPEG taxidermist D. Pimentel, returned to Caxiuanã to obtain specimens of this unrecognized species. We successfully obtained a series of tape recordings and a voucher specimen with voice and tissue samples for future analysis.

I analyzed all catalogued vocalizations of the smaller *Micrastur* species from the Macaulay Library of Natural Sounds (MLNS) at the Cornell Laboratory of Ornithology and the British Library of Natural Sound Archive. I also searched the holdings of the following major natural history collections: Academy of Natural Sciences of Philadelphia (ANSP), Louisiana State Univ. Museum of Natural Science (LSUMZ), Museu Nacional de Rio de Janeiro (MNRJ), Naturhistoriska Riksmuseet Stockholm (NRM), and Museu de Zoologia da Univ. de São Paulo (MZUSP). I identified seven recordings of the new forest-falcon attributed to the other *Micrastur* species and located an additional 22 specimens. I have concluded that these represent a new species of *Micrastur*, and I propose to name it:

Micrastur mintoni sp. nov.
Cryptic Forest-Falcon
Falcão Cryptico (Portuguese)

Holotype.—MPEG 54849; adult female from Estação Cientifica Ferreira Penna, Caxiuanã, Melgaço, Pará, Brazil (01° 44.176′ S, 51° 21.162′ W); at approximately 200 m; 2 August 1999 collected by Dionsío Corrêa Pimentel Neto and tape recorded by AW. Vocal recordings were archived (MLNS 107100–107103) and tissue samples were deposited at MPEG.

Diagnosis.—The most diagnostic feature separating this new cryptic *Micrastur* from all congeners is its voice (see below).

A small raptor (body mass 170–264 g) belonging to the family Falconidae; clearly assignable to the genus *Micrastur*, characterized by short rounded wings, long graduated tail, and a slight, almost owl-like facial ruff (Ridgely and Gwynne 1989). Similar in size and plumage to the monotypic *M. gilvicollis*, but differing in its proportionately shorter tail (a mean of 7.5% smaller) and a different wing: tail ratio (Table 1).

The most important diagnostic plumage character of *M. mintoni* is the tail pattern; adults have one broad white central tail band, and subadults have two broad white to buff tail bands. In contrast, adult and subadult *M. gilvicollis* show two distinctly narrower white tail bands, and immature *M. gilvicollis* have two or three white to buff narrow tail bands. In the field the second (basal) tail band of *M. gilvicollis* often is obscured from view by wing projection (pers. obs.). *M. mintoni* sometimes has an incipient additional second tail band completely covered by the upper tail coverts (13 of 22 MPEG specimens; absent in *M. gilvicollis*). A contrastingly darker forehead, crown, and nape is shown on 50% of *M. mintoni* (all subadult birds except one in the MPEG displayed this feature), whereas only 7% of *M. gilvicollis* showed a contrastingly darker hood. In *M. mintoni*, an eyebrow of bare bright orange skin extends above the whole eye (Fig. 1), whereas in *M. gilvicollis* it extends above only the anterior three-quarters of the eye. From the nares, the distance to the feathering on the forehead is less in *M. mintoni* (mean of 5.49 mm, range 3.49–6.56 mm, $n = 23$) than in *M. gilvicollis* (mean of 6.63 mm, range 5.18–9.15 mm, $n = 13$). The horizontal dark barring on the underparts is bolder on *M. mintoni*, in which the barring is better defined on the breast (especially in females), and extends down to the midbelly and lacks buff wash (Fig. 1). Posterior to the midbelly, in *M. mintoni* the dark barring is absent or greatly reduced (Fig. 1), the bars becoming narrower with wider pale interstices, whereas *M. gilvicollis* shows denser and finer dark barring with less white showing between the bars that typically extends farther down than *M. mintoni* (Fig. 2). Also, *M. gilvicollis* often has

TABLE 1. Morphology of four *Micrastur* forest-falcons; values are means (range, *n*). Wing chord is flattened. *M. gilvicollis* weights ($n = 92$) were from field captures ca 60 km north of Manaus, Amazonas, Brazil and were from unsexed birds.

Sex	Wing chord (mm)	Tail length (mm)	Wing : tail ratio	Body mass (g)
M. mintoni[a]				
Male	183 (175–200, 24)	135 (129–151, 24)	1.36 (1.28–1.46, 24)	200 (171–238, 8)
Female	186 (174–201, 16)	137 (129–145, 14)	1.35 (1.22–1.45, 14)	219 (170–264, 11)
M. gilvicollis[a]				
Male	178 (169–188, 10)	137 (131–150, 11)	1.29 (1.16–1.35, 10)	
Female	182 (177–188, 4)	140 (138–146, 4)	1.29 (1.28–1.32, 4)	209 (170–262, 96)
M. plumbeous[b]				
Male	175 (171–178, 4)	127 (123–134, 4)	1.34 (1.27–1.45, 4)	180 (172–188, 3)
Female	174 (168–182, 9)	130 (115–140, 9)	1.37 (1.30–1.45, 9)	191 (180–213, 4)
M. ruficollis[a]				
Male	170 (164–179, 9)	159 (151–167, 9)	1.06 (1.04–1.12, 9)	
Female	175 (162–190, 17)	164 (153–179, 17)	1.06 (1.00–1.16, 17)	

[a] Data from MPEG, MZUSP, and MNRS.
[b] Data from P. G. W. Salaman (pers. comm.).

an irregular wash or stain of buff on the upper breast (Fig. 2).

The other two small *Micrastur* species differ in plumage as follows. *M. plumbeous* has shorter wings and tail (Table 1); cere, lores, and orbital area are bright flaming red (not orange); irides dark brown in adults and whitish beige (not white) in immatures (P. G. W. Salaman pers. comm.); paler bluish gray upperparts; pale gray throat (not white) with the underparts otherwise entirely barred, with the barring typically darker and bolder. *M. ruficollis concentricus* differs in its shorter wings and longer tail and different wing : tail ratio (Table 1); three narrow tail bands in adults (subadult and immatures have four); cere, lores, and orbital area dull yellow-orange (not orange); irides brownish (not white); and underparts entirely barred except for throat. Nominate *M. ruficollis* displays the same features as those outlined for *M. r. concentricus* above, differing distinctly with a brown (not gray) mantle and a bold striking rufous nuchal collar in adults.

Description of holotype.—See frontispiece and Figures 1–3. Capitalized color nomenclature and corresponding numbers follow Smithe (1975).

Forehead, crown, and nape slightly darker than the back, wings and rump Blackish Neutral Gray (82). Sides of face and neck Dark Neutral Gray (83) with irregular faint traces of fine white grizzling on lower neck caused by white bases to neck feathers.

Cere, lores, nares (both external and internal), and orbital area (including eyebrow) Spectrum Orange (17). Legs and toes nearest to Orange Yellow (18). Claws: basal third nearest to Buff (124) and distal two-thirds Blackish Neutral Gray (82). Upper mandible: basal 4 mm nearest Orange Yellow (18), remainder Jet Black (89). Lower mandible: basal three-quarters nearest Orange Yellow (18), remainder Blackish Neutral Gray (82). Base of bill, cere, and nares with tiny 6- to 9-mm black rictal bristles, some with basal third white under the mandible. Iris white with a slight grayish cast, eyelid Spectrum Orange (17) covered with fine short white feathers.

Chin white. Throat: upper two-thirds white and lower third with fine 0.5-mm Blackish Neutral Gray (82) horizontal barring across the feathers, which becomes gradually bolder, reaching 1.5 mm toward the lower throat. Breast: base color white, each feather finely barred with 5–6 narrow Blackish Neutral Gray (82) bars, forming continuous horizontal bars in a gentle u-shape across the breast, increasing slightly in width and gradually in boldness from the lower throat down to the upper breast, where they reach maximum of 2.5 mm wide; below this the number and width of bars begins to decrease gradually in size to 0.5

FIG. 1. Adult male *Micrastur mintoni*, demonstrating four diagnostic distinctions from the cryptically similar *M. gilvicollis*: (1) the bolder dark barring on the underparts extending down to the midbelly; (2) posterior to the mid-belly, barring is generally absent or greatly reduced; (3) irregular wash of buff on any of the underparts is lacking; and (4) the bare bright orange eyebrow skin extends above the whole eye. Photographed in *terra firme* forest mid-story by W. Carter, September 2002, Alta Floresta, Mato Grosso, Brazil.

mm, with no bars below about the middle of the breast. Flanks and lower belly white and unbarred, stained irregularly with Pale Horn (92), mostly toward the center of the lower belly.

Ventral area white. Tibia: very fine horizontal barring broadly spaced, Dark Neutral Gray (83) across the front of the thighs. Axillars and underwing coverts white, with only the exterior carpel coverts finely vermiculated

with dark Neutral Gray (83) bars. Tail slightly darker than Blackish Neutral Gray (82) but not as dark as Jet Black (89); darker, however than primary and secondary flight feathers. One broad white central tail band 11 mm wide, 55 mm from tail tip and 62 mm from base of the tail. All rectricies with a Pale Horn (92) terminal apical fringe of 1–2 mm. A second incipient white tail band 6 mm wide on the central rectricies hidden under the upper-tail coverts. Undertail Blackish Neutral Gray (82) with central white cross bar. Undertail coverts white.

Measurements of holotype.—Wing (unflattened chord) 193 mm, tail 131 mm, culmen from base (at skull) to cere 16 mm, tarsus 50 mm, hind claw 15.2 mm, total length 342 mm, skull 100% ossified, body mass 225 g, ovary 4 × 2 mm, oviduct 2 mm wide, largest ovum 2 mm. Plumage fresh and unabraided with outer three rectrices on both sides symmetrical in molt.

Description of subadult and immature plumage.—See frontispiece and Figures 3 and 5. Forehead, crown, and nape darker than back on all four subadult females (MPEG 36072, 37965, 52498, and MZUSP 43867). MPEG 36072 exhibited a distinct dark-capped effect due to greatest crown-mantle contrast, closest to Jet Black (89). MPEG 52498 was molting into adult plumage with the darker hood showing much contrasting Plumbeous (78) mixed among Blackish Neutral Gray (82). Six of the seven subadult males (MZUSP 11864, 43869, 42759, 14020, 28055, and MPEG 31428, showed contrast on the crown, mantle, and wings; variation from darkest Blackish Neutral Gray (82) to the palest, nearest Dark Neutral Gray (83).

Bill: two subadult females (MPEG 34933 and 36072) had culmen tipped 7 mm and 4 mm, respectively, Orange Yellow (18), contrasting to the rest of the bill, Jet Black (89). MPEG 37965 had a 4-mm tip to the culmen that was closest to Buff (124), with the rest of the culmen a Blackish Neutral Gray (82). Iris: five subadult specimens (MPEG 36072, 37966, 52498, and two not yet accessioned) were labelled as white and three (MPEG 37965 and two not yet accessioned) were labeled as brown.

Tail: ten subadult specimens (MZUSP 11864, 14020, 28035, 42759, 43867, 43869, MPEG 36072, 37965, 52498, and MNRJ 1472) with Blackish Neutral Gray (82) tail crossed by two broad white tail bands and a well-defined 2- to 6-mm Buff (124) terminal apical fringe. On one subadult (MPEG 43867) the tail was too badly worn for it to be detected. The tail band position varied on all seven subadult specimens (MPEG 37965 and 52489, and MZUSP 43867, 11864, 42759, 14020, and 28035). Measurements (distance of the two bands from the tail tip) were taken on the central rectrix. Distances of first band (nearest point of the band to tail tip) were 48, 49, 54, 50, 53, 42, and 56 mm, respectively. Distances of second band were 92, 91, 112, 91, 106, 90 and 101 mm, respectively. Three subadult males (MPEG 37966, 31428 and 34933) were in advanced stages of body molt, nearing adult plumage and having already acquired the single broad white central tail band of adult plumage. MPEG 34933 had the lowest position of tail band compared to all 16 adult MPEG specimens, only 43 mm from the tail tip.

Possible juvenal male (MPEG 37966) was almost unmarked below (Fig. 5), its white underparts with a Buff (124) stain, with only eight 10-mm-long, 2- to 3-mm-wide horizontal bands, closest to Dark Brownish Olive (129) and restricted to the sides of the upper breast, with only faint traces of the bars in the center. Lower belly, thighs, and flanks were white with Buff (124) stain. The boldest underpart markings were on a subadult female (MPEG 52498) with 3- to 4-mm-wide Blackish Neutral Gray (82) horizontal barring down to the lower breast, with a distinct unbarred 25-mm white wedge in the center of the breast. Three other subadult birds (MPEG 37965, 34933, and 36072) showed substantial reductions in the amount of horizontal barring on the underparts. Subadult male MPEG 31428 showed underparts closest to Pale Horn (92) with fine Dark Brownish Olive (129); horizontal barring extended only one-third of the way down the breast with the lower two-thirds unbarred.

I describe the single presumed immature male (NRM 568416) from a photograph (G. Frisk unpubl. data) with the help of a detailed plumage description Gyldenstolpe (1945). This unique specimen showed a well-marked white spot or half crescent below the auricular

FIG. 2. Ventral barring on *Micrastur mintoni* and *M. gilvicollis*. (1) *M. mintoni* adult female holotype (MPEG 54849), Caxiuanã, Pará, Brazil. (2) *M. gilvicollis* adult male (MPEG 42442), Rio Japurá, Amazonas, Brazil. Photograph by A. Whittaker.

region. Further unique plumage characteristics were the extreme reduction of banding beneath, restricted to only a few narrow, faint, short, Blackish Neutral Grey (82) bars along the sides of the chest; rest of underparts, including throat, were white. The tail feathers had two broad (5 mm) white bands. The lower tail band was below the center of the tail, whereas the upper band was just below the upper tail coverts, i.e., located higher up the tail than in any of the other *M. mintoni* specimens. Underwing coverts and axillars were white without any cross banding.

Sexual dimorphism and variation in para-

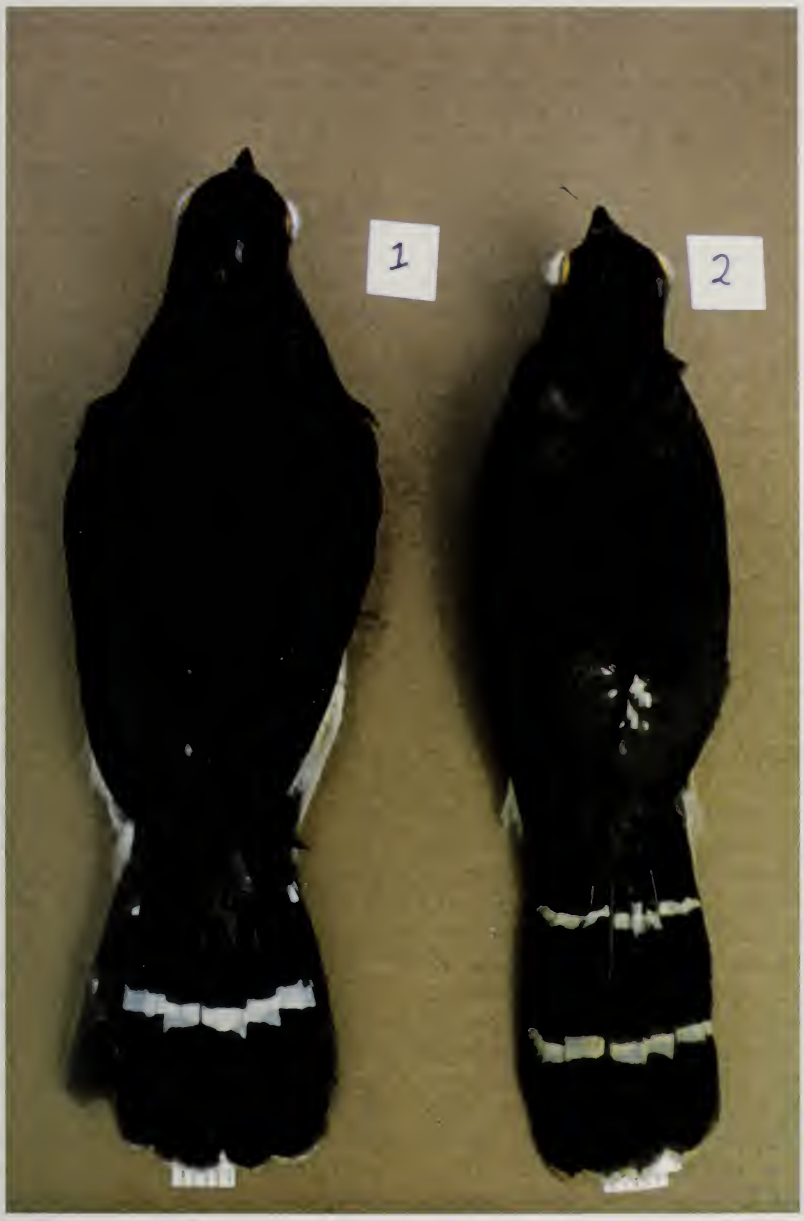

FIG. 3. Tail patterns of *Micrastur mintoni*, illustrating distinct tail barring. (1) Adult female holotype (MPEG 54849), Caxiuanã, Pará, Brazil. (2) Subadult female (MPEG 37965), Maraba, Pará, Brazil. Photograph by A. Whittaker.

types.—The type series of *M. mintoni* consists of 53 specimens: 37 adults (21 male, 16 female), 10 subadults (six male, four female), 1 probable immature male, and 5 unsexed specimens (2 adult, 3 subadult). Although there is great individual variation, sexual dimorphism in *M. mintoni* involves only the extent of ventral barring (Fig. 5), with females generally more boldly barred below than males. Individual variation in mantle color exists but is subtle, the darkest individuals being slightly darker than Blackish Neutral Gray (82), the palest being nearest to Dark Neutral Gray (83).

The single broad central tail band varied from white to a Buff (124), but this variation may be the result of specimen preparation, chemical staining, or the age of older skins. The central tail band varied in width from 5–12 mm and was white to Buff (124). The apical fringe varied from 2–6 mm, and was generally bolder in subadult birds and absent on two adult males and an unsexed adult (possibly due to abrasion); however it also was absent on all specimens with fresh tails (MPEG 28090, 38406 and 34064). Two subadult females (MPEG 34933 and 37966) had an additional second 2-mm subterminal tail band of Buff (124), with the typical 2-mm apical fringe more Gray (83) than Blackish Neutral Gray (82). The incipient second upper tail band was specifically searched for on 23 MPEG skins of the new taxon, and was found present in seven males, five females, and one unsexed specimen.

Iris color was labelled white on 11 adults (MPEG 39331, 39332, 41601, 54849, and LSUMZ 131911 and 136811, MNRJ 6184, and four not yet accessioned) and five subadults (MPEG 36072, 37966, 52498, and two not yet accessioned). These 16 specimens and 20 additional field observations confirm that the normal eye color of *M. mintoni* is white (Fig. 1). However, three subadult specimens, indicating brown irides, strongly suggests that some subadult and immature birds probably have darker irides, similar to the ontogenetic sequence of iris color in other *Micrastur* species (pers. obs.). I conclude that the brown iris of the adult female (MPEG 34933) probably was not a true color due to bloodstaining as this specimen was shot.

Underwing pattern varied from white to Buff (124), with no vermiculation on six adult males (MPEG 32382, 33499, 48490, 39332, 41601, and 37207) and two subadult males (MPEG 31428 and 37966), to having vermiculation restricted to the carpal coverts on five adult males (MPEG 17970, 24263, 28090, 39331, and 38406) and three adult females (MPEG 54849, 48489, and 47661). Adult male MPEG 11591 had extensive dusky bars on the carpel coverts, axillars, and remainder of the underwing. Five subadult females (MPEG 27965, 34933, 36072, 52498, and 11288) showed creamy buff underwings with no vermiculation.

The Atlantic rainforest specimens from eastern Brazil (MNRJ 30548 and MZUSP 11864 and 14020) differed from Amazonian birds as follows. An adult female (MNRJ 30548) had an irregular Buff (124) wash on the breast, whereas the two males, both subadult, were more extensively and heavily barred below. Given the small sample size, it is impossible to determine if this represents individual variation or if this isolated population deserves subspecific status. I suggest that this population's geographic (and thus likely genetic) isolation from Amazonian birds makes it likely that a separate subspecies is involved. More material from this geographical area will need to be located and examined to determine whether this is the case.

Specimens examined.—The material from three institutions (MPEG, MNRJ, and MZUSP) was measured by the author. Flattened wing chord and tail length were measured to the nearest 1 mm with a wing rule with a perpendicular stop at zero. Bill and tarsus measurements were made to the nearest 0.1 mm with dial callipers. Six additional specimens were located outside Brazil (ANSP, LSUMZ and NRM) and are not included in measurement analysis. I compared *M. mintoni* to at least 15 specimens of the other members of the genus *Micrastur*, with the exception of *M. plumbeous* (P. G. W. Salaman unpubl. data).

M. mintoni: (53) BRAZIL: (50). Pará 33: 18 males, 11 females, 4 unsexed birds, Belém area (MPEG 11288, 11591, 28090, 47661, 17970; Km 86 BR 010; MUZSP 42759); Benfica municipal Benevides (MPEG 2426); Bacabá, Capitão Poço (MPEG 31428); Ourém, Rio Guamá (MPEG 32382); Paque Nacional de Tapajós (MPEG 34064); Santa Jacundá, Left bank of the Rio Tocantins (MPEG 36072); Carajás, Serra dos Carajás (MPEG 37207); Marabá, Rio Sororo, CVRD Reserve (MPEG 37965, 37966); Breves, Ilha do Marajó (MPEG 41601); Santana do Araguaia (MPEG 48489–48490); Estação Cientifica Ferreira Penna, Caxiuanã, Melgacão (MPEG 52498, 54849, and six not yet accessioned); one of unknown sex from Altamira (MPEG); Rio Gurupi, Camiranga (MNRJ 1472); Rio Curuá, Iriri (MNRJ 6184); Caxirieatuba (MUZSP 22915); Rio Pracupi, Portel (MUZSP 2071); Capim, BR 14 km 96,

MUZSP 43867–43869). Amazonas: two, a male and female, Lago Batista (MUZSP 18032, MNRJ 21669). Rondônia: two males, Cachoeira Nazaré, west bank of Rio Japaraná (MPEG 39331–39332). Mato Grosso: four, two males, Rio Peixoto de Azevedo (MPEG 33499); Rio Teles Pires (MNRJ 30550); two females not yet accessioned from Rio Juruená (MUZSP). Maranhão: three, two females, one male, Turiaça, Bom Jesus da Mata (MPEG 34932–34933); Acailandiá, Rio Itingá (MPEG 38406). Bahia: two males, Itabuna (MUZSP 11864); Rio Jucurucú, Cachoiera Grande (MZUSP 14020). Espirito Santo: one female, Linhares (MNRJ 30584).

Specimens confirmed by photographs: BRAZIL: (4). Pará: three, a male and female from Aveiro, Rio Tapajos (NRM 568416–56817; G. Frisk pers. comm.), a female from Rio Guama (ANSP 80812), and one of unknown sex and locality in Brazil (ANSP 241; N. H. Rice pers. comm.). BOLIVIA: (2). A male and female, Depto. Santa Cruz (LSUMZ 136811–136812).

M. gilvicollis: BRAZIL: (17). Amapá: eight, five males, three females (MPEG 19797, 20904, 24196, 29079, 16457, 20905, 29071; MNHRJ 29162). Amazonas: six males (MUZSP 28035, MPEG 42441–42442, 46913, 50523, 52946). Pará: three, one male and two females (MPEG 34506, 46913, MNHRJ 6183).

M. ruficollis concentricus: BRAZIL: (21). Pará: nine (MPEG 1500, 3819, 6610, 29686, 35816, 35819, 41601, 46914, 47660). Amapá: three (MPEG 20906, 24834, 47662). Acré: three (MPEG 48031, 48032, 52016). Maranhão: one (MPEG 41946). Mato Grosso: one (MPEG 51274). Rondônia: four (MPEG 39333 and one not yet accessioned, MUZSP 30503, 34945).

Tape recordings examined.—All recordings are by the author unless otherwise stated. I compared all of the three similar (small sized) *Micrastur* species, including the five races of *M. ruficollis*, nominate *ruficollis*, *M. r. concentricus*, *M. r. guerilla*, *M. r. zonothorax*, and *M. r. interstes*, to the *M. mintoni* recordings.

M. mintoni: (42 recordings). BRAZIL: (35). Pará: 17, Melgaço 14; Belém (P. Schwartz, MLNS 59166); Serra dos Carajás (J. F. Pacheco, 1); Amazonia National Park, 1. Mato Grosso: 13, Alta Floresta, 4, (K. J. Zimmer and T. A. Parker, 1; K. J. Zimmer, 1; C. A. Marantz, 1); Rio Cristalino 1, (C. A. Marantz, MLNS 88528–88530, 1 uncatalogued). Rondônia: 4, Serra do Pacaás Novas, 1; Guajará-Mirim, 2; Cachoiera Nazare (T. S. Schulenberg, MLNS 43364). Amazonas: Borba, 1. BOLIVIA: (7). Depto. Santa Cruz.

M. gilvicollis: (76 recordings). BRAZIL: (33). Amazonas: 29, 18, (T. A. Parker, MLNS 80425; C. A. Marantz, MLNS 88303–88306; P. Schwartz, MLNS 59167–59170, 59172; M. Cohn-haft, 1). Amapá: 3. Acré: 1. PERU: (16). Loreto: 6, 4, (M. B. Robbins, MLNS 37400; J. V. Moore, 1). Madre de Díos: 10, 1, (T. A. Parker, MLNS 24113, 24269, 24279, 29437, 29573, 29439, 29710; P. Donahue, MLNS 55837; A. B. Van den Berg, MLNS 28968). GUYANA: (6). Essequibo: (M. B. Robbins, MLNS 85812, 85757). Rupununi: (D. W. Finch, MLNS 89863, 89877; T. A. Parker, MLNS 70021, 73048). VENEZUELA: (14). Bolivar: (P. Schwartz, MLNS 59153, 59163, 59164). Río Grande: 10 (P. Schwartz, MLNS 59154–59162, 59165). Amazonas: (K. J. Zimmer 1). ECUADOR: (5). Prov. Napo: (K. J. Zimmer, 2; R. A. Rowlett, MLNS 84458; J. V. Moore, 2). BOLIVIA: (2). Depto. Beni: (A. B. Hennessey, MLNS 88004). Depto. La Paz: (T. A. Parker, MLNS 52325).

M. ruficollis: (179 recordings). BRAZIL: (49). Rondônia: 5, 3, (T. S. Schulenberg, MLNS 43374, 43774). Amazonas: 3 (P. Schwartz, MLNS 59136, 59149); Acré, 1. Rio de Janeiro: 6, 4, (T. A. Parker, MLNS 22136, 32049). Bahia: 1. Paraná: 3. Rio Grande do Sul: 15, 4, (P. Schwartz, MLNS 18852, 59132–59134; G. A. Bencke, MLNS 88095, 90113; W. Belton, MLNS 18848, 19855, 25421; F. Silva, MLNS 25444, 25447). Mato Grosso: 4, 3, (C. A. Marantz, MLNS 88377). Minas Gerais: 3. Pará: 2, 1, (S. M. Fonseca, 1). São Paulo: 2 (P. Schwartz, MLNS 59130–59131). Espírito Santo: 2. VENEZUELA: (63). Aragua 31: (P. Schwartz, MLNS 59085–59087, 59090–59091, 59098–59103, 59106, 59110, 59119–59123, 59127–59129, 59137–59142, 59144–59145, 59148, 59151). Tachira: 6 (P. Schwartz, MLNS 59088–59089, 59124–59126, 59143). Bolivar: 20 (P. Schwartz, MLNS 59092–59097, 59104–59105, 59107–59109, 59111–59118; L. Macaulay, MLNS 60936). Merida: 5 (D. Macdonald, MLNS

FIG. 4. Tail patterns of male and female *Micrastur gilvicollis*. (1) Adult male (MPEG 52946), Manaus, Amazonas, Brazil. (2) Adult male (MPEG 42442), Rio Japurá, Amazonas, Brazil. (3) Adult female (MPEG 16547), Rio Iratapura, Amapa, Brazil. (4) Adult female (MPEG 46913), Porteira, Pará, Brazil. Photograph by A. Whittaker.

44252, 44255; P. Schwartz, MLNS 59146–59147; D. Fisher, MLNS 55728). Amazonas: 1 (P. Coopmans, MLNS 68139). PERU: (18). Lorento: 2, 1, (M. B. Robbins, MLNS 37399). Madre de Díos: 12 (T. A. Parker, MLNS 11498, 23808, 23816, 29700, 29581, 29809; C. A. Marantz, MLNS 76005–76006, 76136, 76375; P. Donahue, MLNS 55838; J. W. Fitzpatrick, MLNS 43128). Cuzco: 2 (A. Begazo, MLNS 85071, 85334). Pasco: 1 (T. S. Schulenberg, MLNS 35875). Amazonas: 1 (T. A. Parker, MLNS 17571). ECUADOR: (15). Esmeraldas: 4 (M. B. Robbins, MLNS 48928, 48942, 48971; T. A. Parker, MLNS 80233). Pichincha: 3 (P. Coopmans, MLNS 58021, 58041; M. B. Robbins, MLNS 49103). Chical: 1 (M. B. Robbins, MLNS 49199). Mindo: 1 (L. Macaulay, MLNS 63454). Sucambo: 1 (M. B. Robbins, MLNS 74698). Morona: 3 (T. S. Schulenberg, MLNS 36037, 39953; M. B. Robbins, MLNS 41272); El Oro, 1 (M. B. Robbins, MLNS 43465). Manabi: 1 (T. A. Parker, MLNS 71852). COLOMBIA: (2). Santa Marta: 2 (P. Coopmans, MLNS 68062, 68059). BOLIVIA: (12). La Paz: 5 (T. A. Parker, MLNS 13808, 13843, 13886; G. Cox, MLNS 90860; A. B. Hennessey, MLNS 87617). Beni: 2 (A. B. Hennessey, MLNS 87821, 88036). Pando: 1 (T. A. Parker, MLNS 38386). Santa Cruz: 3 (T. A. Parker, MLNS 51934, 52455; G. Cox, MLNS 90189). Tambo: 1 (R. A. Rowlett, MLNS 85600). GUYANA: (1). Rupununi: 1 (T. A. Parker, MLNS 70052). PARAGUAY: (1). Canideyú: 1 (À. Madrono, MLNS 91959). ARGENTINA: (1). Salta. PANAMA: (2). Darien: 2 (T. A. Parker, MLNS 25819, 25859). COSTA RICA: (13). Limóa: 4 (C. A. Marantz, MLNS 76648–76651). Puntarenas: 7 (D. Ross, MLNS 53905, 55082, 55240, 55186; B. [?? MI?] Spencer, MLNS 31408, 31412; C. A. Marantz, MLNS 76107). Guanacaste: 1 (T. A. Parker,

FIG. 5. Age variation in ventral barring of *Micrastur mintoni*. (1) Adult female holotype (MPEG 54849), Caxiuanã, Pará, Brazil. (2) Adult female (MPEG 34933), Turiacu, Maranhao, Brazil. (3) Subadult female (MPEG 37965), Maraba, Pará, Brazil. (4) Possible juvenal male (MPEG 37966), Maraba, Pará, Brazil. Photograph by A. Whittaker.

MLNS 32334). Las Cruces: 1 (T. A. Parker, MLNS 39304). GUATAMALA: (1). (J. C. Roché, MLNS 59150). BELIZE: (5). Toledo, 5 (T. A. Parker, MLNS 71051, 71076, 71841, 71844, 71848). MEXICO: (1). Chipas: 1 (C. O. B. Hanks, MLNS 95071).

Etymology.—I take great pleasure in naming this species in honor of my good friend Clive D. T. Minton in recognition of his major contribution to our understanding of shorebird biology and their conservation worldwide. Clive was a major influence in teaching me ornithology during my childhood and later became my bird-banding trainer and mentor. His never-ending enthusiasm for the study of birds and their conservation was contagious and has inspired many. The English and Portuguese names call attention to the forest-falcons cryptic plumage, which caused this new species to be overlooked for nearly a century, despite being represented in leading museum collections worldwide.

REMARKS

Systematics.—Since the formation of the genus *Micrastur* (Gray 1841), the systematics of the smaller forms, particularly those inhabiting the Amazon Basin, has been the subject of considerable controversy. Hellmayr (1910) was the first to suggest that there were in fact two small species in the *M. ruficollis* complex, concluding that *M. gilvicollis* was a valid species. He later changed his mind (Hellmayr 1929). After re-examining specimens, Hellmayr and Conover (1949) reverted to treating *M. gilvicollis* as a valid species. Meyer de Schauensee was equally indecisive, first (1966) recognizing *M. gilvicollis* as a valid species, but later (1970) retracting this and considering it conspecific with *M. ruficollis*. Pinto (1935, 1947, 1964), Phelps and Phelps (1958), and Haverschmidt (1968) also treated *M. gilvicollis* as a species separate from *M. ruficollis*. Schwartz (1972) finally presented

conclusive vocal and biometric evidence demonstrating that *M. gilvicollis* was indeed a valid species, sympatric with *M. ruficollis* across much of its range.

Historically, several ornithologists had puzzled over the complex plumage variation in small *Micrastur* forest-falcons, particularly from Brazil. Gyldenstolpe (1945), in reviewing the Olalla collection from the Rio Juruá, Amazonas, Brazil, compared two *M. gilvicollis*, a male (NRM 568421) and a female (NRM 568422), with five other supposed *M. gilvicollis* specimens: a male and female from Aveiro, Pará (NRM 568416–568417), and Casa Nova, Pará (NRM 568418–568419), and one female from Lagoa Baptista, Amazonas (NRM 568420). Gyldenstolpe was especially puzzled by NRM 568416, noting its remarkable plumage and its exceptionally small size, particularly its short (134 mm) tail. Gyldenstolpe concluded a correct understanding could be reached only by examination of a very large series from all parts of their range. I conclude after studying photographs and measurements of the NRM specimens (G. Frisk pers. comm.) that this puzzling small male *Micrastur* (NRM 568416) is a *M. mintoni* in immature plumage. I also confirm that (NRM 568417) is an adult *M. mintoni*. Gyldenstolpe surely was further confused by this series because *M. gilvicollis* (NRM 568422) is a *M. ruficollis concentricus*.

Neumann (1933) was the first to claim that certain short-tailed individuals from Brazil (Bahia and Pará) with a single tail band were conspecific with *M. plumbeous* of western Ecuador. Hellmayr, in a personal note to Gyldenstolpe, also discussed the possibility of the Pará birds being *M. plumbeous* (G. Frisk pers. comm.). Intent on solving the problem, Hellmayr and Conover (1949) re-examined specimens from the Vienna and Berlin museums, comparing them with the puzzling Aveiros skins (NRM 568416–568417) at the British Museum of Natural History collection, concluding that they occupy an intermediate position between *M. gilvicollis* and *M. plumbeous*. They also noted the existence of other Pará specimens with two tail bands, contradicting the notion that all Pará birds have but a single tail band. This was an oversight, because Pará state extends both north and south of the Amazon; *M. gilvicollis* occurs north of the Amazon in Pará and only *M. mintoni* occurs south of the Amazon. *M. gilvicollis* occurs in Brazil on the south bank of the Amazon only west of the Rio Madeira in Amazonas, Acre, and extreme western Rondônia.

More recently, the taxonomic status of the short-tailed Pará birds was noted by Amadon (1964), who stated concerning *M. gilvicollis*, "the tail is shorter than any of the other small *Micrastur* (except *M. plumbeous*); and in some cases, especially in Brazilian Amazon, as on the Rio Madeira and Rio Tocantins, the basal of the two tail bars is lacking or is concealed by the upper tail coverts." Nearly a decade later Schwartz (1972) noted that the addition of material from Brazilian museums increased the overlap in his wing : tail ratios of *M. gilvicollis*. In fact, he had included several specimens that now have been demonstrated to represent *M. mintoni*.

M. plumbeous is found only in the foothill forests of southwestern Colombia and northwestern Ecuador (Ridgely and Greenfield 2001), having an entirely disjunct distribution from that of *M. gilvicollis*. *M. plumbeous* has been found to be sympatric and even syntopic with *M. r. interestes* in both Colombia (P. G. W. Salaman pers. comm.) and Ecuador (R. S. Ridgely pers. comm.). The taxonomic history of *M. plumbeous* is almost as convoluted as that of *M. mintoni*, both having been confused with *M. gilvicollis*. Meyer de Schauensee (1966) suggested that *M. plumbeous* would best be considered a separate species if *M. gilvicollis* were recognized as distinct from *M. ruficollis*, as suggested by Amadon (1964). However subsequent to Schwartz's (1972) recognition of *M. gilvicollis* as a distinct species, most authors did recognize *M. plumbeous* as a valid species (e.g., Hilty and Brown 1986). Recent work in Colombia has demonstrated unequivocally that *M. plumbeous* is indeed a valid species (P. G. W. Salaman pers. comm.).

Early taxonomists thus had noted several perplexing plumage and morphological features on certain small *Micrastur* specimens, features that included a single broad tail band, shorter tail, and variation in breast markings. However, due to ongoing confusion with the taxonomy of *M. ruficollis* (with which *M. gilvicollis* was still widely regarded as conspecific) and to a lesser degree with *M. plum-*

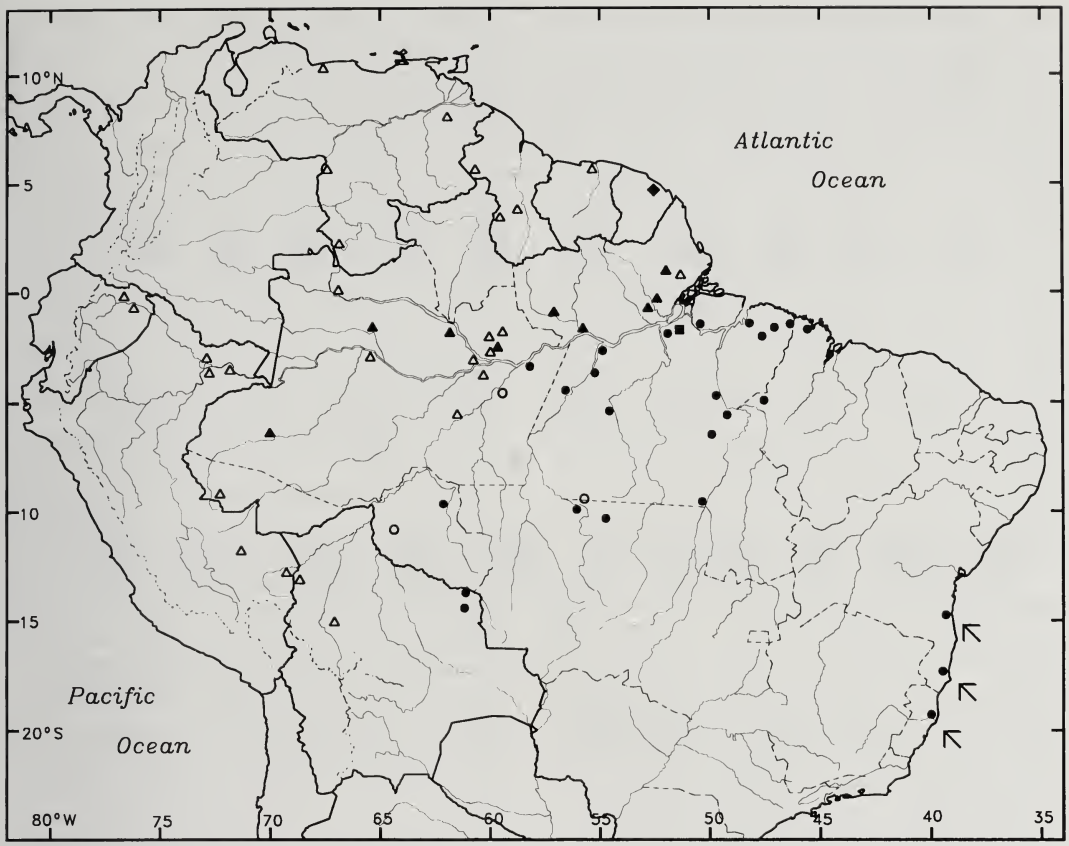

FIG. 6. Distributions of *Micrastur mintoni* sp. nov. and *M. gilvicollis*. All localities are confirmed by specimens or tape recordings examined by the author. (solid square) Type locality of *M. mintoni*, Caxiuanã; (open circles) locality documented by voucher tape recording; (solid circles) locality documented by either a voucher specimen or by both a voucher specimen and tape recording. (solid diamond) Type locality of *M. gilvicollis*, Cayenne, designated by Hellmayr (1910); (open triangles) locality documented by voucher tape recording; (solid triangles) locality documented by either a voucher specimen or by both a voucher specimen and tape recording. Map by M. L. Isler.

beous, no one suspected that an entirely new species was actually involved. They all lacked an important piece of the puzzle that modern field workers have: first hand field experience with these birds and especially their vocalizations. It was the markedly different voice of this new *Micrastur*, combined with my extensive field experience with the vocal repertoires of *M. gilvicollis* and *M. ruficollis* across most of their respective ranges, that initially enabled me to single out this new, cryptic species.

Distribution.—M. mintoni is known from southeastern Amazonia, with its range south of the Amazon River and east of the Rio Madeira extending into the Brazilian states of Amazonas, Pará, and Maranhão south into Mato Grosso and southwest into Rondônia, extending just into adjacent northeastern Bolivia in northern Depto. Santa Cruz. A second range-restricted population is known from eastern Brazil, from southern Bahia into northern Espírito Santo north of the Rio Doce (Fig. 6). *M. mintoni* is found in Amazonian lowlands up to about 600 m, as in Carajas, Pará, Brazil.

Habitat.—Specimens, tape recordings, and observations of *M. mintoni* all are from humid tropical rainforest. Recent observations indicate that the principal habitat for *M. mintoni* is *terra firme* forest. This forest type is characterized by a high diversity in tree species,

tall canopy with height of about 30–35 m with occasional emergents, and a dense understory with many palms, vines, and epiphytic plant species. The *terra firme* forest in Noel Kempff Mercado National Park, Bolivia, differs from the forests farther east in having lower tree diversity and being almost devoid of epiphytes (this presumably due to lower annual precipitation and greater temperature variation). *M. mintoni* also frequents seasonally flooded forests with two Brazilian sight records, one from Pará and the other from Rondônia, and a specimen from Bolivia. Both Brazilian records were of single birds in low stature (15–20 m) seasonally flooded *igapo* forest (black water flooded forest). In Depto. Santa Cruz, Bolivia, LSUMZ 136812 was collected in *varzea* (white water flooded forest) with much bamboo in the understory.

Vocalizations.—Territorial displays of many Neotropical forest raptors involve soaring above the forest proclaiming their territorial presence by vocalizing, often combined with a flight display. *Micrastur* spp., on the other hand, never soar (Thorstrom et al. 2000a); vocal activity within the forest is their only means of long range communication to conspecifics. Thus, voice probably is important in species recognition in this genus. All *Micrastur* species have evolved a distinctive species specific repertoire, which includes three main vocal types, which I describe as follows. (1) The "territorial advertising song" is the most commonly heard vocalization in all *Micrastur* species and therefore the most well known. (2) The "excited cackling call" is the second most commonly heard vocalization, regularly heard in response to tape playback. This vocalization is quite similar among species, especially between *M. gilvicollis* and *M. r. concentricus*. (3) The "quacking song" is heard mostly from one of a pair during a duet (rarely heard in the field); however, sometimes one bird or one of a pair responds using this voice to tape playback. The complex vocal repertoire found within each species of *Micrastur* has led to great confusion in voice identification (Whittaker 2001), which has resulted in many errors in identification of *Micrastur* specimens to species level.

Peak vocal activity for *M. mintoni*, as for all other *Micrastur* species (Thorstrom 1993, Klein and Bierregaard 1988, Whittaker 2001), is 20–30 min prior to dawn. A less important peak occurs just before dusk; the species is seldom heard at other times of the day. Long range communication in diurnal birds typically is concentrated in the early morning (Hanwood and Fabrik 1979). *Micrastur* species are among the first birds to be heard in the morning in any Neotropical forest because their series of low frequency notes is ideal for traveling long distances through these dense forests at this time, when background noises are at a minimum. Vocal activity may be weather dependent, with reduced vocal activity associated with overcast conditions (pers. obs.). Seasonal variation in vocal activity has not been quantified; I have noted seasonal changes in *M. gilvicollis*, i.e., periods of intensified vocal activity at the onset of the rainy season (presumed to be their early breeding season).

I include herein a description of all known vocalizations of *M. mintoni*, as well as spectrograms of the other three small *Micrastur* species. The territorial advertising song (Figs. 7A, 8A–8D, 9A, 10A–10B) is the most commonly heard vocalization of *M. mintoni*. This song consists of single low-pitched notes repeated at about 1 note per second, "UK, UK, UK, UK, . . . ," with each note "swallowed." The repetitions may continue for an extended period, with a short gap of 3–5 s between song bouts. The number of "UK " notes varies individually, in some bouts as many as 273 notes and lasting about 2.5 min. Typical bouts include 120–150 notes and last from 1–1.5 min. Short song bouts, however, may include as few as 18 notes. This song is most frequently heard from a single bird vocalizing during pre-dawn. The initial song bout usually starts at a low volume, increasing gradually, until the typical volume is achieved. At a distance this song could be confused with those of certain frogs. Occasionally I have heard the territorial advertising song as an antiphonal duet (Fig. 7F), during which the pair remains widely separated. During such duets, I have noted slight differences in pitch in the "UK" notes; the slightly higher-pitched bird presumably is the smaller male (Fig. 10A; see female in Fig. 10B).

The excited cackling call (Fig. 7B) is a series of short, fast, cackled "CA" notes that speed up and sound like a bouncing object going downscale, "CA,CA,CA,CA-CA-

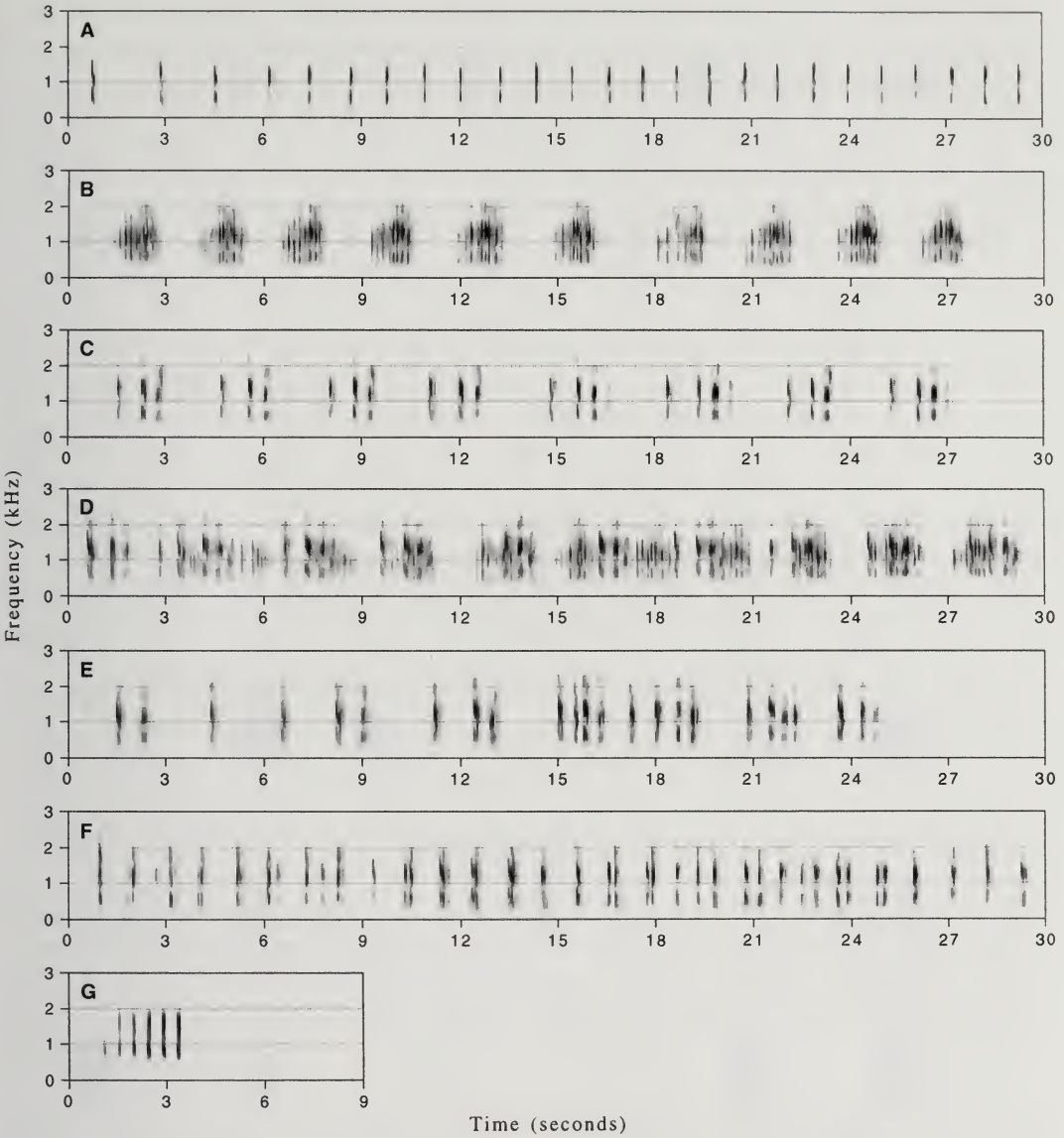

FIG. 7. Vocalizations of *Micrastur mintoni*. Recordings are by the author except as noted. (A) Territorial advertising song, Caxiuanã, Pará, Brazil, 29 October 1997, MLNS 10704. (B) Excited cackling call from the holotype (MPEG 54489), Caxiuanã, Pará, Brazil, 2 August 1999, MLNS 107102. (C) Quacking song, Alta Floresta, Mato Grosso, Brazil, 10 September 1999, MLNS 107107. (D) Duet, in which one bird begins with quacking song and mate responds with excited cackling calls; Caxiuanã, Pará, Brazil, 2 August 1999, MLNS 107102. (E) Territorial duet, including the holotype (MPEG 54849), showing both birds using quacking song, but with a different number of notes; Caxiuanã, Pará, Brazil, 2 August 1999, MLNS 107102. (F) Antiphonal duet of pair singing territorial advertising song; Alta Floresta, Mato Grosso, Brazil, 24 August 1991 (to be archived at MLNS); recorded by Kevin Zimmer. (G) Unusual response to tape playback of a territorial advertising song, Rio Cristalino, Alta Floresta, Mato Grosso, Brazil, 19 October 1997, MLNS 88529; recorded by C. A. Marantz. Spectrograms by P. R. Isler.

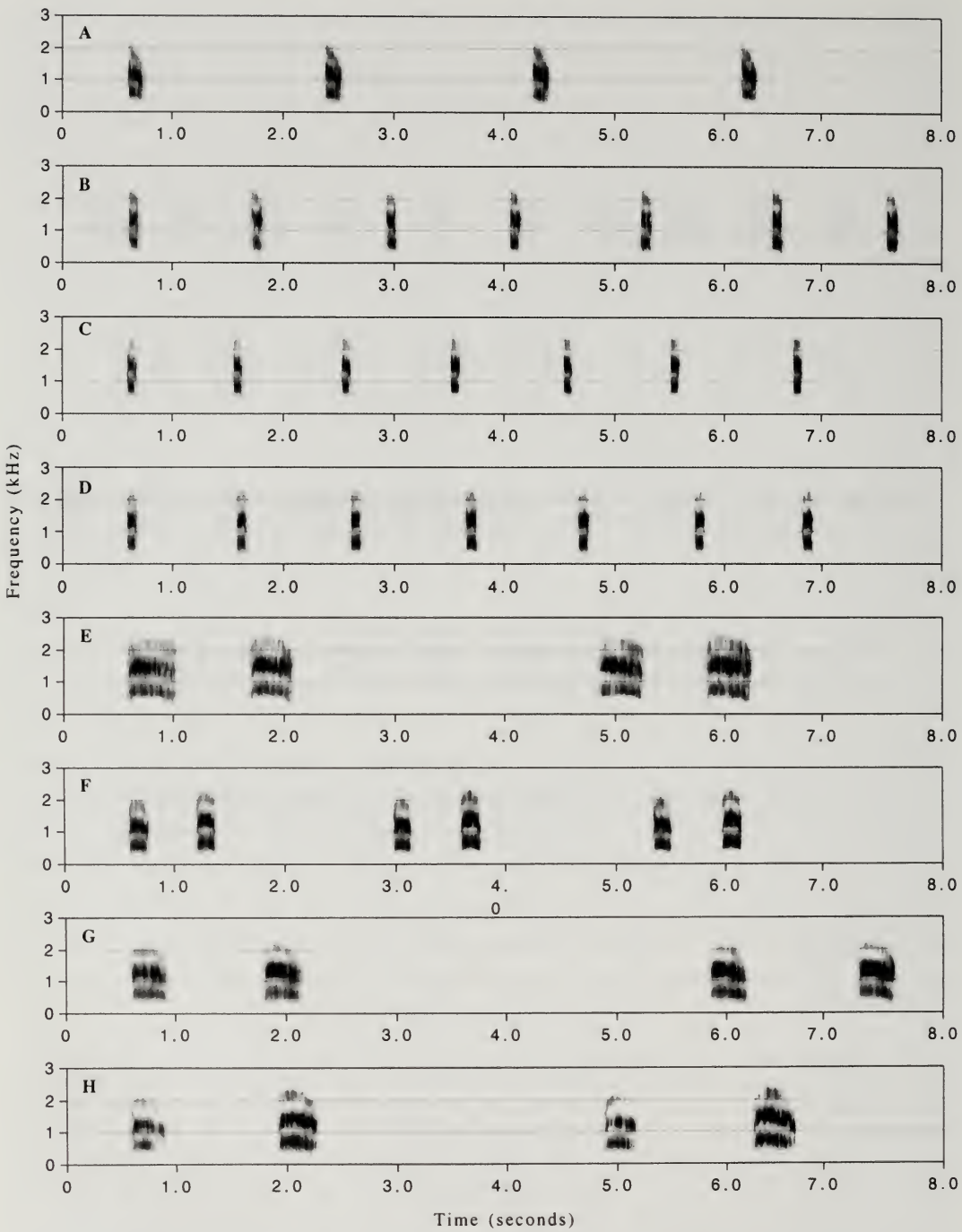

FIG. 8. Territorial advertising songs of *Micrastur mintoni* and *M. gilvicollis* from geographically widespread localities. Recordings are by the author except as noted. (A–D) *M. mintoni*. (A) One of the pair of the holotype (MPEG 54849), Caxiuanã, Pará, Brazil, 2 August 1999, MLNS 107102. (B) Alta Foresta, Mato Grosso, Brazil, 11 September 1999, MLNS 107105. (C) Parque Nacional da Amazônia, Pará, Brazil, 7 June 2000, MLNS 17106. (D) Parque Nacional Noel Kempff Mercado, Depto. Santa Cruz, Bolivia, 17 July 2000, MLNS 17108. (E–H) *M. gilvicollis*. (E) Maipaima Creek Rupununi, Guyana, 5 February 1993, MLNS 70021; recorded by T. A. Parker. (F) Aceer, Dept. Lorento, Peru, 19 April 1999, MLNS 10721. (G) Tambopata, Dept. Madre de Dios, Peru, 17 June 1982, MLNS 29439; recorded by T. A. Parker. (H) Careiro do Castanho, Amazonas, Brazil, 3 December 2000, MLNS 107109. Spectrograms by P. R. Isler.

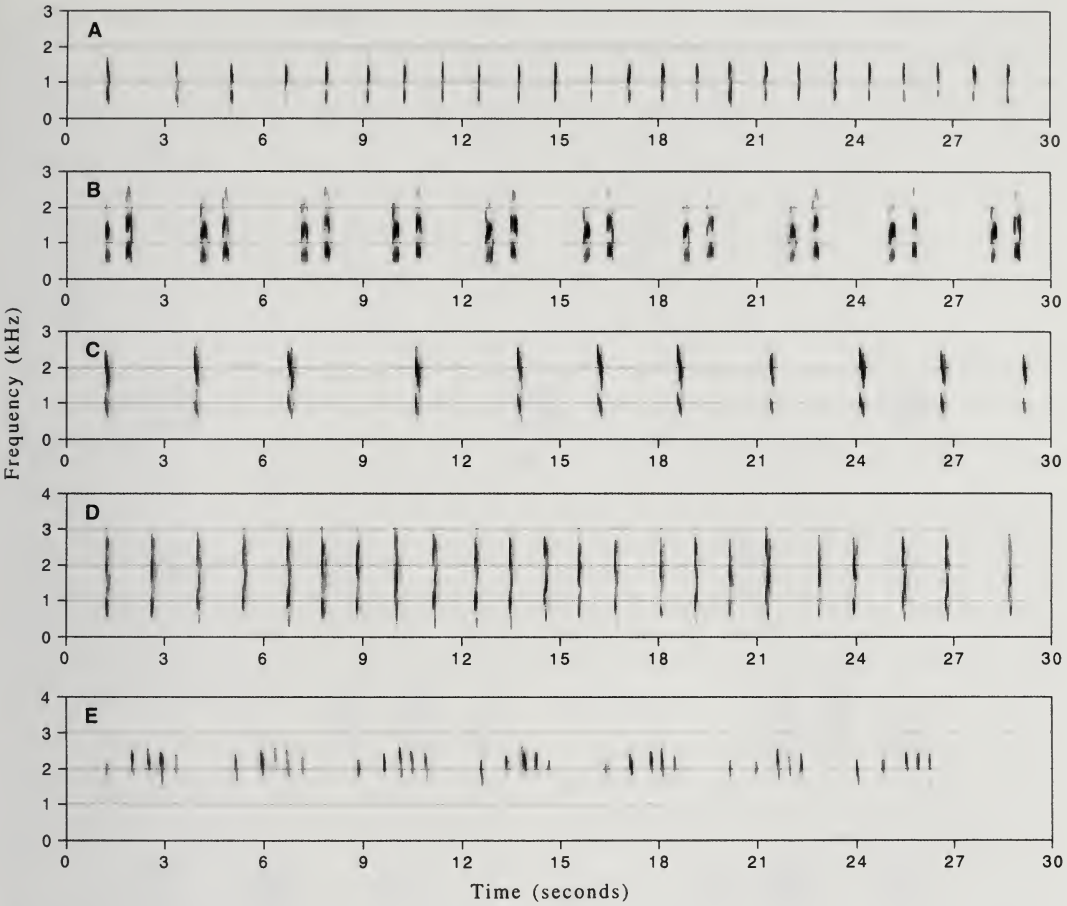

FIG. 9. Territorial advertising songs of all small *Micrastur* species. Recordings by the author except as noted. (A) *M. mintoni*, Caxiuanã, Pará, Brazil, 29 October 1997, MLNS 107104. (B) *M. gilvicollis*, Balbina, Amazonas, Brazil, 19 December 1999, MLNS 107111. (C) *M. r. concentricus*, Rio Cristalino, Mato Grosso, Brazil, 14 September 1998, MLNS 107112. (D) *M. r. ruficollis*, Parque Nacional do Itatiaia, Rio de Janeiro, Brazil, 23 October 1999, MLNS 107113. (E) *M. plumbeous*, Narino, Colombia; recorded by P. G. W. Salaman. Spectrograms by P. R. Isler.

CA′CA′CA′. . . . " These calls are repeated every 1–2 s, and calling bouts last from 45 to >60 s. The first four notes are emitted rapidly, and the following notes given even faster, with the last few notes decreasing slightly in speed. One variation to this pattern was a bird adding six deep "UR" notes before resuming a typical excited cackling call.

The quacking song (Fig. 7C) consists of a series of three loud, lamenting notes, "UUK, QUI, QUA" that lasts about 1.5 s and gradually progresses to a four-note "UUK, QUI, QUA-QUA," which lasts about 2 s. These series of notes are repeated every 1.5–2 s during 1.0- to 1.5-min song bouts. Toward the end of long song bouts a bird sometimes reverts back to three notes. Agitated birds responding to tape playback may add an initial 1–2 more emphatic "UUK" notes to the sequence, giving 5–6 notes (Fig. 7E). Once I recorded an unusual two-note "QUI, QU" call repeated 18 times during 30 s before the bird reverted to the typical quacking song.

The territorial duet of a pair (mostly heard in response to tape playback) begins when the first bird to approach utters the excited cackling call, often beginning by calling very quietly before gaining in volume. The mate then joins in with a territorial advertising song, often from a distance, although later it usually

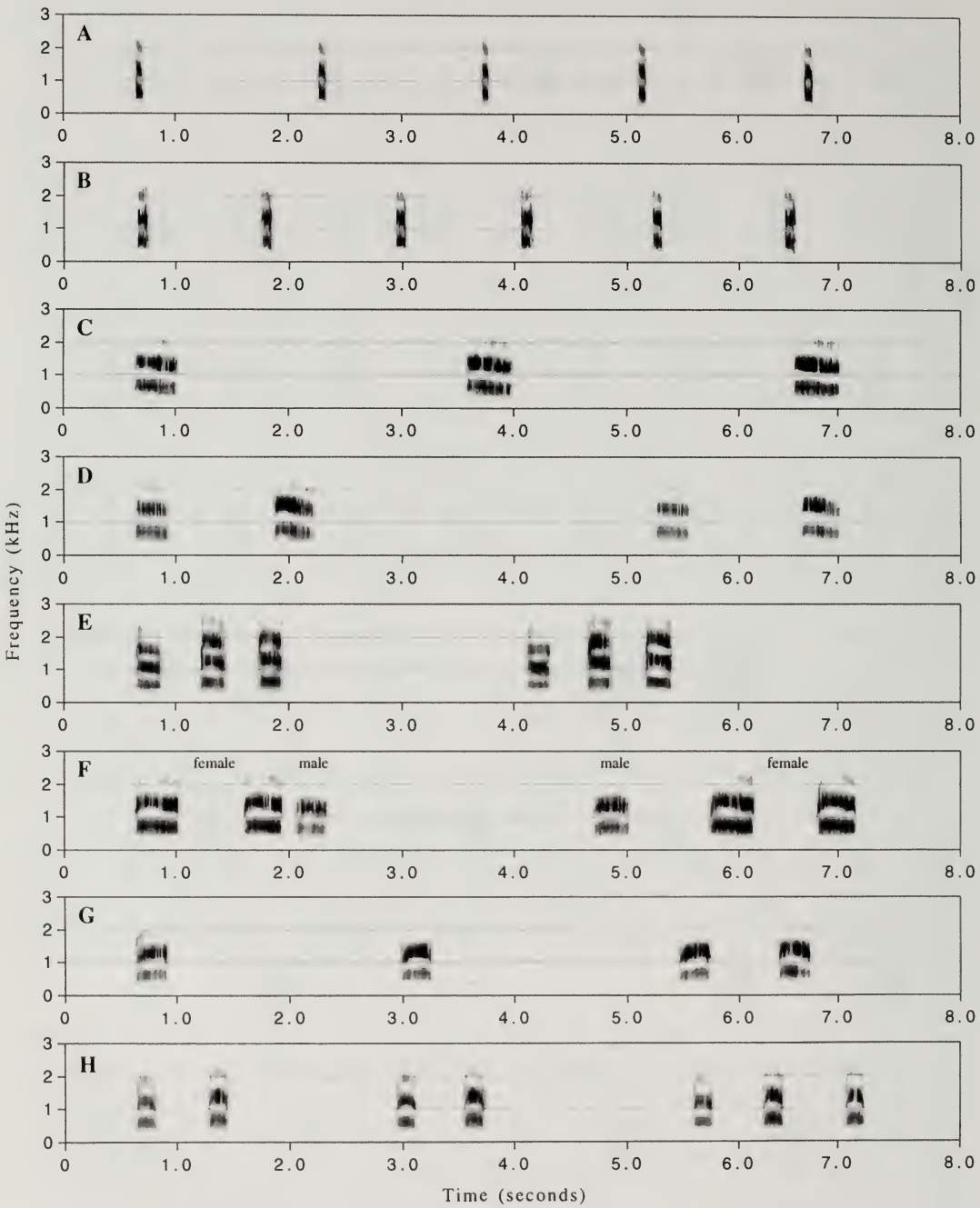

FIG. 10. Territorial advertising songs of *Micrastur mintoni*, showing sexual variation, and *M. gilvicollis*, showing variation in the number of notes. All recordings are by the author. (A–B) *M. mintoni*. (A) Territorial advertising song of a presumed male, Alta Floresta, Mato Grosso, Brazil, 11 September 1999, MLNS 107114. (B) Territorial advertising song of a presumed female, Alta Floresta, Mato Grosso, Brazil, 11 September 1999, MLNS 107115. (C–H) *M. gilvicollis*. (C) One-note song, São Gabriel do Cachoiera, Amazonas, Brazil, 11 August 1999, MLNS 107116. (D) Two-note song, São Gabriel do Cachoeira, Amazonas, Brazil, 11 August 1999, MLNS 107117. (E) Three-note song, Uara, Rio Solimoes, Amazonas, Brazil, 8 September 1992, MLNS 107118. (F) One- and two-note song duet, Balbina, Amazonas, Brazil, 19 December 99, MLNS 107119. (G) One-note changing to two-note song, Balbina, Amazonas, Brazil, 19 December 1999, MLNS 17120. (H) Two-note changing to three-note song, Aceer, Lorento, Peru, 19 April 1999, MLNS 107121. Spectrograms by P. R. Isler.

approaches. Then one member of the pair switches to a typical quacking song and its mate then follows with the excited cackling call, the two alternating forming a rhythmic duet (Fig. 7D).

An unusual series of quiet, guttural, frog-like croaks (MLNS 88529, 88530; Fig. 7G) in response to tape playback of a territorial advertising song was recorded by C. A. Marantz. Another unusual voice in response to tape playback (not shown by sonogram) was a short series of 3–5 "hoo" calls between the excited cackling calls; this sounded very similar to a call of *Tigrisoma lineatum* (Rufescent Tiger-Heron).

There is no known tape recording of the disjunct population of *M. mintoni* from the Atlantic rainforests of eastern Brazil. During an intensive two-day search using tape playback during peak vocal activity (pre-dawn and pre-dusk) in Espírito Santo in April 2000, I surveyed about 15 km of trail in humid lowland Atlantic rainforest at Linhares CVRD reserve and failed to encounter the species.

For comparison with *M. mintoni*, I present *M. gilvicollis* territorial advertising song (the most commonly heard voice), consisting of a loud, lamenting, two-note bark (Figs. 8E–8H, 9B, 10D). This two-note song is repeated regularly at intervals of generally 3–5 s for several minutes. Two variants of the main two-note pattern are heard regularly. (1) The song can be initiated as repeated single note every 2–4 s during early pre-dawn (Fig. 10C), later changing into the typical two-note song (Fig. 10G). (2) The two-note song can progress to a three-note song towards the end of song bouts (Fig. 10H).

A comparison of 42 different *M. mintoni* recordings with 76 *M. gilvicollis* (from a wide geographical distribution) confirmed that *M. mintoni* showed a consistent diagnostic difference in all its vocal types from *M. gilvicollis*. Furthermore, no geographical variation in voice was apparent in either of these two species (Fig. 8). The sonograms of the other congeners, *M. r. concentricus* (Fig. 9C), *M. r. ruficollis* (Fig. 9D), and *M. plumbeous* (Fig. 9E), also demonstrate their strong vocal differences from *M. mintoni*. However, I did find a consistent strong vocal difference between nominate *M. r. ruficollis* and *M. r. concentricus* (Fig. 9C, 9D) and suggest that this complex warrants further taxonomic research.

Because voice is taxonomically informative, I conclude that *M. mintoni* is a valid species because of subtle but consistently distinctive morphology, diagnostic voice (see Fig. 11), and parapatric distribution from the cryptically similar *M. gilvicollis*.

Systematics.—Comparison of vocal similarities in sibling species has been used effectively to demonstrate species limits (Isler et al. 1997, Krabbe and Schulenberg 1997). The territorial advertising song of *M. plumbeous* is a repeated series of five notes (Fig. 9E) that sounds very similar to the quacking song of *M. mintoni* (Fig. 8E); further vocal comparison was not possible due to the very small vocal sample of *M. plumbeous*. However, this vocal similarity, combined with several shared plumage characters (shorter tail, distinctive single broad central tail bar of adults), leads me to predict that the closest species to *M. mintoni* may be the geographically distant *M. plumbeous*.

Behavior and ecology.—M. mintoni is an inconspicuous and elusive forest dependent raptor. Consequently, almost nothing is known of its natural history. Although the species is a year round resident of Neotropical rainforest, the structure of the forests and the bird's secretive and shy nature makes field observations of this *Micrastur* extremely difficult. Birds rarely were observed by chance. I did observe a bird perched on a bare branch 30 m high in the canopy of *terra firme* forest at Arequiemes, Rondônia, Brazil, on 28 January 1995 at 15:00. I presumed it was drying out in the afternoon sun because it had rained hard since dawn, stopping only about 30 min earlier.

On another occasion at 12:50 on 8 July 2002 at Guajara-Mirim, Rondônia, Brazil, in secondary growth bordering virgin *terra firme*, I observed *M. mintoni* attending an army-ant (*Eciton* sp.) swarm. An area of the understory bordering the trail had been recently cleared by farmers; here an adult bird flushed from the floor, landing 2 m high on a horizontal branch above the swarm. The ant swarm was attended by *Rhegmatorihina hoffmannsi* (White-breasted Antbird), *Dendrocincla merula* (White-chinned Woodcreeper), *D. fuliginosa* (Plain-brown Woodcreeper), and

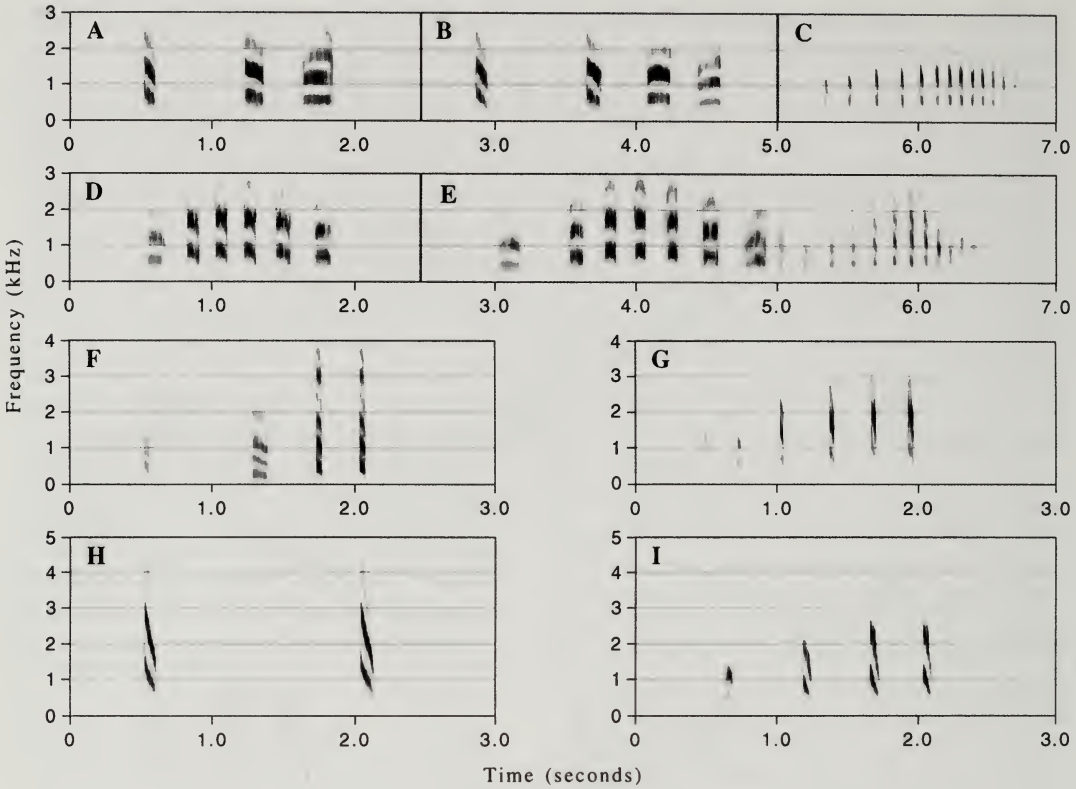

FIG. 11. Comparison of the calls of all small *Micrastur* species. Recordings by author except as noted. (A–C) *M. mintoni*. (A) Three-note quacking song, Alta Floresta, Mato Grosso, Brazil, 10 September 1999, MLNS 107107. (B) Four-note quacking song, Alta Floresta, Mato Grosso, Brazil, 10 September 1999, MLNS 107107. (C) Excited vibrating cackling call from holotype (MPEG 54849), Caxiuanã, Pará, Brazil, 2 August 1999, MLNS 107100. (D–F) *M. gilvicollis*. (D) Excited cackling call, Balbina, Amazonas, Brazil, 19 December 1999, MLNS 107124. (E) Excited cackling call and vibrating cackling call, Balbina, Amazonas, Brazil, 19 December 1999, MLNS 107125. (F) Excited cackling call in response to extended playback, Balbina, Amazonas, Brazil, 19 December 1999, MLNS 07126. (G) *M. plumbeous*. Excited cackling call, Narino, Colombia; recording by P. G. W. Salaman. (H) *M. ruficollis concentricus*. Excited cackling call, Reserva Ducke, Amazonas, Brazil, 6 November 1995, MLNS 10727. (I) *M. r. ruficollis*. Excited cackling call, Parque Nacional de Itatiaia, Rio de Janeiro, Brazil, 23 October 1999, MLNS 107128. Spectrograms by P. R. Isler.

Cnemotriccus fuscatus (Fuscous Flycatcher); none exhibited an apparent response to the raptor's presence. The *Micrastur* still-hunted from its perch above the swarm, occasionally bobbing its head while intently looking down at the forest floor. After about 5 min it flew down diagonally about 15 m, landing on a dead stump 30 cm above the ground. Almost immediately it dropped to the floor and ran quickly out of sight, presumably pursuing a prey item. Ant swarm attendance also is documented for four other *Micrastur* species, including *M. ruficollis*, *M. gilvicollis*, *M. semitorquatus* (Collared Forest-Falcon), and *M. buckleyi* (Buckley's Forest-Falcon), which were observed feeding on fleeing arthropods and lizards (Willis et al. 1983, Mays 1985, Whittaker 2001).

On 13 September 2000, 10:30, at Rio Cristalino, Alta Floresta, Mato Grosso, Brazil, N. Zeide watched a bird as it flew to a perch 15 m high in the mid story of *terra firme* forest and from there tore at an unidentified prey item held in its talons. A minute later another bird landed within 5 m of the first bird. Moments later they both flew away together, and what sounded like a food-begging call was heard from that direction.

Most observations of *M. mintoni* were obtained by tracking down vocalizing birds; tape

playback of their voice (especially during predawn) greatly increases the chances of encounters. A combination of a ventriloquil quality of their calls and the dense habitat makes it difficult to locate even vocalizing birds. Upon closer approach, birds frequently stop singing, remain silent, then flush from their concealed perch and silently fly away, most often unseen by the observer. Typically in response to playback, a pair of territorial birds will approach, at first silently, usually unseen by the observer, and minutes later start calling. Continued tape playback generally induces one of the pair to approach more closely, often with a direct fast flight through the midstory, with a characteristic *Accipiter*-like flight pattern (a few quick, deep wing beats followed by a short glide). Vocalizing *M. mintoni* perched mostly on large horizontal boughs, often close to a tree trunk, typically 10–20 m high in the midstory. Occasionally, I have found vocal birds lower (3–5 m) in the understory. At dawn and dusk however, they often go higher into the canopy and subcanopy to vocalize.

During singing bouts, *M. mintoni* moves its body, wings, and tail slightly in synchrony with each note. The head also is gently jerked about 10–15° upward from the horizontal as each note is emitted. Individuals do not necessarily remain on the same song perch during song bouts, often moving to new perches in response to vocal neighboring birds or tape playback. On arrival at a perch in response to playback, a bird often would lean forward, craning its head and neck, peering around to locate the intruder. Birds also run agilely for short distances along boughs to a better vantage point or to turn through 180° on a perch in search of the vocal intruder. On one occasion, upon my approach a singing bird hopped to a higher perch where it repeatedly quivered its tail. I also noted this behavior in *M. gilvicollis* in response to tape playback of its voice. Both *M. r. ruficollis* and *M. gilvicollis* may produce audible wing clapping. *M. gilvicollis* on initial take off, and *M. r. ruficollis* during horizontal flight, each produced loud wing claps at a volume similar to some *Columba* spp. during wing-flapping flight displays (pers. obs).

Until recently little was known about the behavior of any *Micrastur* species because they are so difficult to locate. However, recent intensive fieldwork in Guatemala by Thorstrom (1993) and Thorstrom et al. (2000a, 2000b) has added greatly to our knowledge. Recent information on the behavior of the other small *Micrastur* may provide some inference about *M. mintoni* behavior. Thorstrom (1993) and Robinson (1994) found that *M. ruficollis* hunts by surprise attacks from low, concealed perches. Robinson (1994) watched a *M. ruficollis* that was perched inconspicuously 2 m above the ground, still-hunting along the edge of a forested clearing, catch two lizards 15–20 cm long. Robinson (1994) also observed the same behavior in *M. gilvicollis*, still-hunting in low understory <10 m high. In Brazil I observed an *M. gilvicollis* still-hunting, perched 2.5 m high in shaded forest understory, searching the forest floor. Klein and Bierregaard (1988) observed four radio-marked *M. gilvicollis* for a total of 67 days north of Manuas, Brazil, and concluded that they perched during the day from 6–8 m high on vines or understory plants. These data are contrary to the hypothesis of Willis et al. (1983) that *M. gilvicollis* was primarily a canopy species. Klein and Bierregaard (1988) found that *M. gilvicollis* typically remained in one area without moving more than 50 m during 1–3 days. Recent field work on the poorly known *M. plumbeous* (P. G. W. Salaman pers. comm.) found that it has two main foraging methods: (1) foraging actively on the ground, running after prey with tail held high, and using their long legs to grasp prey with their feet; and (2) still-hunting from low (usually <2 m high) perches, searching the leaf litter for movement and sound, and then pouncing on prey.

Until recently the diet of the small *Micrastur* species was thought to be birds (Hilty and Brown 1986, Ridgely and Gwynne 1989). However, raptors that prey primarily on very maneuverable prey such as birds tend to be highly sexually dimorphic (Thorstrom et al. 2000a) and also have relatively long toes (Bierregaard 1978). These adaptations are found in the larger *M. semitorquatus*, in which females are 48% larger (Thorstrom et al. 2000a). This is not the case in *M. mintoni*, which exhibits none of these morphological adaptations. I suspect that *M. mintoni* will prove to be a generalist, eating a variety of reptiles and small

invertebrates. The specialized narrow, curved, stiff feathers forming the small ear ruff may be used to improve auditory detection of prey. This feature, combined with their large eyes, perhaps enhances hunting ability using a sit-and-wait strategy from a low perch in the poorly lit understory. Stomach contents of two male *M. mintoni* (MPEG 39332 and MNRJ 1472) each contained a single large unidentified arthropod, and the latter also contained a lizard. These data support the generalist hypothesis.

Research on *M. ruficollis* in Guatemala (Thorstrom et al. 2000a) revealed that of 405 identified prey items, reptiles were predominant (61.5%), followed by birds (22.0%), insects (8.2%), mammals (mostly small rodents; 5.9%), amphibians (2.5%), and snakes (1.1%). Fruit eating behavior was recorded for *M. ruficollis* on two occasions (Thorstrom 1996). No detailed studies have been made on the diet of *M. gilvicollis*; however, stomach contents from MPEG included a grasshopper, a coleopteran, a small lizard, a 2-cm land snail, and a large unidentified arthropod. Robinson (1994) reported cockroach, hylid tree frog, and insect remains in the stomach. Schwartz (1972) reported bird nestlings, arachnids, insects, and lizards as food items in Venezuela. During mist-netting studies in Manaus, *M. gilvicollis* regularly was captured following small passerines into the nets; however, this presumably was opportunistic feeding behavior (pers. obs.). The main food of *M. plumbeous* is lizards (P. G. W. Salaman pers. comm.).

Population and sympatry.—I found *M. mintoni* to be fairly common but easily overlooked, although it occurs at a rather high density, similar to its sibling species *M. gilvicollis* and *M. plumbeous*. I located 3–4 pairs using tape playback experiments during pre-dawn in Depto. Santa Cruz, Bolivia, along a 1,000-m transect in *terra firme* forest. Research in *terra firme* forest in Brazil and Peru (Klein and Bierregaard 1988, Robinson 1994) on *M. gilvicollis* produced estimates of territory sizes for a pair from 20–67 ha and 40–50 ha. Similarly, mean territory size of four radio-marked pairs of *M. plumbeous* in Colombia was 35–40 ha (P. G. W. Salaman pers. comm.). Robinson (1994) stated "generalists searching for small vertebrates and insects from concealed perches tend to be the most abundant diurnal raptors. These raptors exploit lower trophic levels, where more food is likely to be available."

Several species of *Micrastur* typically are found sympatrically in *terra firme* forest. *M. mintoni* at Caxiuanã was sympatric with *M. ruficollis concentricus*, *M. semitorquatus* and *M. mirandollei* (Slaty-backed Forest-Falcon). I have recorded as many as five species of *Micrastur* occurring sympatrically in *terra firme* in Acre, Brazil (Whittaker 2001). *M. mintoni* was strongly associated with undisturbed *terra firme* forest with dense understory, whereas *M. r. concentricus* seemed to prefer disturbed forest types, both natural secondary growth and man made, including bamboo and more open seasonally drier forest on rocky outcrops.

Breeding and molt.—Direct observation of breeding by *M. mintoni* have not been recorded. Recent information on *M. ruficollis* and *M. semitorquatus* confirmed cavity nesting, and only the females are known to incubate (Mader 1979, Thorstrom et al. 2000a, Thorstrom 2000b). Nest cavities for these two species were located mostly in natural cavities in live trees; however, nesting also occurred in cavities excavated by other animals, and there is one report of *M. ruficollis* nesting in a hole in a cliff (Baker et al. 2000). An adult female *M. mintoni* (MPEG 36072) collected on 4 June showed heavily abraded tips of all rectrices, suggesting that the tail was damaged in a nesting cavity. These data suggest that *M. mintoni* also might be a cavity nester and that the female (MPEG 36072) may well have been in breeding or post breeding condition. Excessive rectrix wear also has been interpreted as indicating cavity breeding in *M. gilvicollis* (Bierregaard 1994). In Guatamala, *M. ruficollis guerrilla*, similar in size to *M. mintoni*, laid two or three eggs; courtship through post-juvenile dispersal lasted 20 weeks, coinciding with the wettest time of the year. I expect that *M. mintoni* also schedules its breeding during the wet season (December to May) when availability of invertebrates and reptiles are highest.

Molt during April to August has been confirmed in *M. mintoni*. An adult female (MPEG 34932) collected on 22 July was molting both primaries and rectricies. Similar tail molt was

recorded from several specimens (MPEG 28090, 48490, 54849) on 22 April, 30 July, and 2 August.

Conservation.—Deforestation is occurring within the range of *M. mintoni* at an alarming rate in southeastern Amazonian Brazil, particularly in the states of Pará, Mato Grosso, and Rondônia. The following national parks, reserves, and indigenous reserves are found within the species' range. Bolivia: Depto. Santa Cruz: Parque Nacional Noel Kempff Mercado. Brazil: Pará: Floresta Nacional de Caxiuanã, Reserva Floresta Gorotiré, Reserva Floresta Mundurucánia, Florestal Nacional do Tapajós; Amazonas: Parque Nacional de Amazônia; Rondônia: Reserva Biológica do Jaru, Parque Nacional de Pacaás Novos, Reserva Biológica do Guaporé; Mato Grosso: Parque Indigena do Xingu. At Caxiuanã, the type locality, the Museu Paraense Emílio Goeldi has established the Estação Cientifica Ferreira Penna. This reserve is bordered by the Floresta Nacional de Caxiuanã; together they form an important area of preservation of 330,000 ha of primarily *terra firme* rainforest that protects not only this new species but also many other threatened species, such as *Guaruba guarouba* (Golden Parakeet) and other fauna and flora of the Pará center of endemism. I see no apparent threat in the near future to the Amazonian population of *M. mintoni*. However, deforestation is continuously destroying vast tracts of pristine habitat, especially in the Brazilian states of Pará, Mato Grosso, and Rondônia. Many Brazilian parks and reserves are well marked on maps but lack management or protection.

The status of the disjunct population in eastern Brazil is critical, if not already extinct. The Atlantic rainforests have suffered some of the most extensive deforestation of any Neotropical rainforest, with only 5–10% of their original area remaining. The single protected area here is in Bahia, the Parque Nacional de Monte Pascoal. Continued hunting by the indigineous people, and poor management of the reserve, makes the situation precarious. The last record for this population was a bird collected in Rio Jucuruçu, Cachoeira Grande, Bahia, on 20 March 1933, by O. M. O. Pinto. Surveys need to be conducted in eastern Brazil as soon as possible to assess the species' status.

DISCUSSION

During the past decade there have been several remarkable ornithological discoveries of new taxa involving overlooked cryptic species (e.g., Schulenberg and Parker 1997, Whitney et al. 2000, Zimmer et al. 2001). Without exception, the discovery of these new species was first made in the field by voice identification. Subsequent searching of museum collections for the new cryptic species always resulted in confirmation that specimens already were present, but had been previously overlooked or were incorrectly identified. This dramatic discovery of yet another new cryptic species should encourage more critical attention to the possibility of more cryptic species yet undiscovered. A much closer revision of existing material in museum collections of Neotropical birds, and particularly those in the less visited South American museums, is strongly encouraged. A better understanding of our cryptic biodiversity would allow for a more accurate cataloging of global biodiversity and would help in the future conservation of many as yet unknown species.

Greater understanding of Neotropical vocalizations during the past two decades has helped to revolutionize Neotropical ornithology. It is an important tool for taxonomic reevaluation of species limits in many Neotropical groups (Isler et al. 1998), and has led to exciting discoveries of new taxa (e.g., Pierpont and Fitzpatrick 1983; Willis 1992; Bierregaard et al. 1997; Zimmer 1997; Zimmer and Whittaker 2000a, 2000b). This recent focus on the importance of vocal behaviors as taxonomic characters has been especially focused on suboscines species. I predict that vocalizations will prove equally important as taxonomic characters in some nonpasserines, in which vocalizations are innate.

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REPRODUCTIVE BIOLOGY OF CANYON WRENS IN THE FRONT RANGE OF COLORADO

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ABSTRACT.—Canyon Wrens (*Catherpes mexicanus*) occur throughout the semiarid regions of the western United States in habitats dominated by canyons and steep rock formations. Their inaccessible habitat has made them one of the least studied among North American birds. We studied a population of Canyon Wrens in the Front Range of Colorado, documenting many aspects of their breeding biology. We report on territory density and size, nest site characteristics, nesting phenology, nesting success, and nestling development. *Received 3 May 2002, accepted 15 November 2002.*

Canyon Wrens (*Catherpes mexicanus*) are found locally in semiarid regions of the western United States in habitats dominated by rocky substrates such as canyons, escarpments, and other areas with precipitous formations (Jones and Dieni 1995). Inaccessibility of their habitat has made Canyon Wrens one of the least studied among North American birds (Jones and Dieni 1995, Johnston 1998). Consequently, we undertook a study to obtain baseline information on this species in an effort to learn more about its reproductive natural history. In this paper, we present observations of a Canyon Wren population in central Colorado, including territory density and size, nest site characteristics, nesting phenology, nesting success, and nestling development.

METHODS

Our primary study site was located at Red Rocks Amphitheater and Mountain Park, situated in the Front Range uplift zone of the Rocky Mountains, 20 km southwest of Denver, Colorado (39° 40′ N, 105° 12′ W; elevation 1,890 m). This site encompassed 1,093 ha, including 280 ha of rock outcrops ≤140 m in height. Exposed substrates are dominated by red, arkosic sandstone and conglomerate rock outcrops of the Pennsylvanian Fountain formation, flanked by Precambrian metamorphic gneiss and schist of the Idaho Springs formation, with Lyons formation sandstone at the base (Taylor 1999). The climate is continental and semiarid; mean annual precipitation is approximately 41 cm for the region. Daily high and low temperatures were a mean of 7 and −8° C, respectively, for January, and 30 and 14° C, respectively, for July (1962–2000, Lakewood weather station; data from Western Regional Climate Center, Desert Research Inst.). We also obtained reproductive data from a second site located near Evergreen, in the interior foothill region of the Front Range (39° 38′ N, 105° 21′ W; elevation 2,380 m).

We conducted breeding surveys from April to September during 1994, 1996, and 1999–2001 and winter surveys from November 1999 to February 2002. We surveyed suitable habitat at Red Rocks Park weekly using tape playback broadcasts of Canyon Wren songs and calls. Once sighted, an individual bird was followed visually and its locations mapped. We determined territory size by plotting boundaries from a mean of 23 (range = 6–68) locations during breeding surveys and a mean of 10 (range = 4–25) locations during winter surveys. We calculated density as the number of territories per 100 ha of rock cover.

We conducted nest searches during the breeding seasons of 1999–2001 using observation and behavioral cues (Martin and Geupel 1993). Once located, nests were monitored every 2–4 days to completion; we documented nesting phenology, clutch size, and number of young fledged. For behavioral observations, we identified the sex of the adults by behavior. Sex was presumed only when both members of the pair were visible and sex was apparent by behavior (e.g., male song).

Nest measurements included nest height (from ground to center of nest), nest rock height, nest site type (e.g., cavity, crevice), nest site slope, and nest and nest site orientation. We used Rayleigh's test (Zar 1999) to test for circular uniformity in orientation of nest and nest site entrance ($P < 0.05$). Several nests were inaccessible and this is reflected in the different sample sizes reported for individual measurements. Measurements for inaccessible nest rocks and nest entrances were estimated where possible using a clinometer and range finder.

RESULTS AND DISCUSSION

Territory density and size.—Summer territory density at Red Rocks Park was con-

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TABLE 1. Characteristics of nest sites and rocky nest substrate for Canyon Wrens in the Front Range of Colorado, 1999–2001.

Statistic	Height of nest (m)	Height of nest rock (m)	Nest height/ rock height ratio	Circumference of entrance (cm)	Entrance area (cm^2)	Cavity volume (cm^3)
Mean	6.7	13.5	0.49	55.5	435	1200
Range	0.8–18.4	1.4–40.4	0.06–0.88	24.4–51.6	47–3200	63–5100
n	16	16	16	10	10	10

sistent among years, with a mean of 4.5 per 100 ha (SD = 0.5, n = 4 years). Summer territory size was more variable, ranging from 0.4–2.8 ha across all years (mean = 1.3 ha ± 0.6 SD, n = 5 years). Winter densities were lower (3.4 per 100 ha ± 0.3 SD, n = 3 years), and territories were smaller, ranging from 0.2–1.9 ha across all years (mean = 1.0 ha ± 0.4 SD, n = 4 years). The smaller mean winter territory size could be a result of their lower responsiveness to tape playback during the winter.

Comparing our estimates of territory size and the total area of rock cover at Red Rocks Park suggests that apparently suitable habitat was not being occupied every year. Territory size likely was underestimated, although this alone cannot account for the discrepancy. One hypothesis is that winter survival may be limiting population size. We observed a 17% decline in summer territory density at Red Rocks Park between the breeding seasons of 2000 and 2001. Areas used for territories in some years were not always occupied during successive years; we observed a mean occupation rate of 57% (n = 14) across years (n = 5).

Nest sites.—Nests (n = 28) always were placed in rocky substrates, predominantly the large outcrops from the Fountain formation, but they also were placed in the smaller rocks and boulders occurring at the base of these outcrops. The use of smaller-sized rocks (<2 m^2) as nest sites (25%, n = 7), was in agreement with the findings of Johnston (1998) in southern Idaho. Nests (n = 21) were placed in an enclosed, protected space, which included 12 (57%) in rock cavities, 6 (29%) in crevices, 2 (10%) in tubes, and one (5%) on a ledge inside a cave. Of these nest sites, 12 (57%) were on vertical rock faces, 3 (14%) on sloping rock <50°, 5 (24%) in groups of smaller rocks, and one (5%) on an isolated small rock. Three nests (14%) also occurred in caves or in multiple rocks that formed a cave-like structure, and six (29%) had protective rock overhang that extended 2–18 cm above the nest site.

There was no apparent pattern of nest placement with respect to available rock height, suggesting that microsite characteristics alone determined nest site selection (Table 1). Nest sites had a mean southern orientation of 158° (z = 3.48, P = 0.028). In contrast, nest entrance orientation did not differ significantly from what would be expected by chance from a uniform distribution (z = 0.21, P = 0.81). Southern orientation of nest sites undoubtedly confers thermal benefits with direct exposure to solar rays during the spring months. However, enclosed nest sites such as rock cavities and crevices may moderate hot outside air temperatures that occur during the summer months. Nest site microhabitats were found to be cooler than outside temperatures during the summer months in Idaho (Johnston 1998). In our study, all nests were protected from direct sunlight and were sheltered from wind and rain.

Nest characteristics.—During 1999–2001, we located and monitored 20 nests at Red Rocks Park. We also report data from an additional eight nests that we opportunistically located between 1993 and 2000. Two (7%) of the nests (n = 28) were reused during the same year, five (18%) in subsequent years, and two (7%) during three consecutive years. Eight (29%) of the pairs had second broods during the same year, and one successfully fledged a third brood. We observed six nests (21%) being torn down by an adult after the young fledged, and the contents were scattered below the nest site.

All nests contained a twig base, interconnected with various plant fragments, including dead leaves and seeds. This base served as

TABLE 2. Reproductive data for Canyon Wrens in the Front Range of Colorado, 1999–2001.

Statistic	Clutch size	Brood size	Number of fledglings per successful nest	Number of fledglings per nest	Incubation period (days)	Nestling period (days)	Total nesting period (days)
Mean	4.5	3.9	3.6	2.9	16.9	16.9	37.5
SD	0.9	0.8	1.0	1.3	1.4	1.7	3.2
Range	2–6	2–6	2–6	2–6	13–19	12–19	29–41
n	22	21	23	28	17	17	15

foundation for a soft cup nest, which contained moss, feathers, and animal hair. In addition, we also observed artificial fragments such as paper, plastic, lint, yarn, and even a rubber band. Mean weight of the soft cup (n = 4) was 26.5 g.

Nesting phenology and nesting success.—Clutches (n = 23) were initiated between 23 April and 15 August, 1994–2001, although breeding has been documented as early as 20 March in Colorado (Jones 1998). Median clutch initiation date was 17 May, with the peak on 15 May (range = 23 April to 26 June). Reproductive data are presented in Table 2.

Of the nests we monitored (n = 28), 22 (79%) successfully fledged young, 2 (7%) had unconfirmed outcomes but were thought to be successful since we observed fledglings in the area, and 4 (14%) failed. Of the nests that failed, two were depredated, one was destroyed by climbers, and one failed due to weather. Renesting occurred ≤7 days following failure for all failed nests. We found two nests that had only the twig bases constructed and were not used further, suggesting that they might be surplus ("dummy") nests similar to the unused nests constructed by other species of the family Troglogytidae (Brewer 2001). This behavior has not been documented previously for Canyon Wrens.

Nestling development.—We documented the development of nestlings at two nests. After hatching, nestlings were altricial, pink, weak, with their eyes closed (Appendix). Near the nests, females used a previously undocumented call (Jones and Dieni 1995) that resembled a rolling buzz, a deep *grrrrr*. The female increased her use of this call as the nestlings neared fledging. We observed fledging at three nests. On all three occasions, fledging began within the first 2 h of dawn. It took ≤2 h for all young to leave the nest for the first flight, and throughout the morning they returned to the nest frequently. They returned to the nest site at night to roost for ≤2 days after fledging. Once fledged, they remained under parental care ≤21 days. During this period fledglings continued to call, using high pitched *cheeps* that resembled the adult alarm call. We observed the male care for the fledglings early in the breeding season, while the female established another nest. The male and fledglings gave alarm calls continuously.

Our data provide much needed information on the basic aspects of Canyon Wren breeding biology. However, since these data may not be representative of all Canyon Wren populations, replication of this study is warranted for other populations throughout this species' range. It would be of interest to make comparisons between populations in the northern extremes and the southern interior to determine how nest site habitat relationships and nesting phenology vary according to parent substrate, land form, and climate.

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APPENDIX. Canyon Wren nestling development, n = 2 nests and 6 nestlings, from Red Rocks Park, Morrison, Colorado, June and July, 2000.

Day	Characteristics
Days 1–2	At hatching, head bent down, legs stretched forward, nestlings resting largely on belly, which is conspicuously distended and remains so for the first few days. Skin grey-pink; eyes closed, grey to blackish-grey; bill and feet pink; egg tooth light yellow-white; mouth lining bright yellow; down grey, in sparse tuffs on crown. No feather tracts. Weight: 2.15 g.
Day 3	Eyes closed, grey. Feather tracts: dorsal and alar raised black dots, ventral faint yellow dots; capital and caudal not evident. Weight: 3.30 g.
Day 4	Egg tooth gone. Feather tracts: dorsal raised black dots; alar pin feathers faint, 0.5 mm; ventral faint yellow dots; caudal not evident; capital with grey down. Weight: 6.90 g. Gape: 9.34 mm; culmen: 6.45 mm; tarsus: 10.10 mm; total length: 37.68 mm.
Days 6–7	Skin pink to dark pink; eyes open, blue-black; mouth lining light yellow to orange. Feather tracts: dorsal pin feathers 1.75 mm, longest primary sheath 3.93 mm, greater coverts 5.07 mm; ventral light-grey dots raised 0.1 mm; caudal barely visible, slightly raised. Weight: 7.70 g. Gape: 10.19 mm; wing chord: 15.51 mm; tarsus: 13.99 mm, total length: 47.14 mm.
Day 9	Faint calls. Skin pink; grey down on head and back. Feather tracts: dorsal, alar, and capital broken. Dorsal: feather 1.31 mm, sheath 3.50 mm; longest broken primary (LBP) feather 0.5 mm, sheath 11.03 mm. Sheaths: capital: 2.74 mm; greater coverts: 3.57 mm; ventral: 2.87 mm; caudal: 3.86 mm. Weight: 7.80 g. Gape: 11.17 mm; wing chord: 21.28 mm; tarsus: 19.19 mm; total length: 47.55 mm.
Day 10	Chipping calls. Eyes black. Weight: 9.20 g. Gape: 12.76 mm; culmen: 7.77 mm; tarsus: 20.88 mm; wing chord: 27.00 mm; 6th rectrix: 8.05 mm; total length: 54.30 mm.
Days 11–12	Loud, high pitched begging calls, crouching, movement away from observer. Bill and feet grey-pink; mouth lining light yellow to orange. All feather tracts broken. Weight: 12.00 g. Wing chord: 37.76 mm; tarsus: 20.6 mm; 6th rectrix: 13.84 mm; total length: 51.91 mm.
Days 14–15	Skin dark grey-pink; eyes all open, iris dark brown; bill and feet pinkish-brown; mouth lining light yellow; gape bright yellow. All feather tracts complete. Fat high. Weight: 12.50 g. Culmen: 7.31 mm; wing chord: 38.17 mm; tarsus: 22.2 mm; LBP: 14.60 mm; rectrices: 15.48 mm; 6th rectrice: 13.98 mm; total length: 61.75 mm.
Day 17	Day before fledging. Skin pink; eyes black; mouth lining yellow-orange. All feather tracts complete and all with sheathing, plumage pattern adult-like, but looser, with down and more white spotting on breast. Weight: 11.23 g. Culmen: 9.39 mm; wing chord: 40.15 mm; 3rd primary, feather: 24.52 mm, sheath: 14.79 mm, LBP: 16.29 mm; tarsus: 23.81 mm; 6th rectrix 15.20 mm, sheath 6.68 mm, total length 63.21 mm.

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GRASSLAND BIRDS ORIENT NESTS RELATIVE TO NEARBY VEGETATION

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ABSTRACT.—We studied orientation of nest sites relative to nearby vegetation for dabbling ducks (Cinnamon Teal, *Anas cyanoptera*; Blue-winged Teal, *A. discors*; Gadwall, *A. strepera*; Mallard, *A. platyrhynchos*; and Northern Shoveler, *A. clypeata*) and Short-eared Owls (*Asio flammeus*) in ungrazed grassland habitat during 1995–1997 in westcentral Montana. We estimated an index of vegetation height and density in intercardinal directions (NE, SE, SW, NW) immediately around nests. All species oriented nests with the least vegetation to the southeast and the most vegetation to either the southwest or northwest. Furthermore, maximum vegetation around nests shifted from the southwest to the northwest with increasing nest initiation date, apparently as a response of individuals tracking seasonal change in the afternoon solar path. Thus, nests were relatively exposed to solar insolation during cool morning hours but were shaded from intense insolation in the afternoon throughout the breeding season. We suggest that nest microhabitat was selected in part to moderate the thermal environment.
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Natural selection should favor nest sites that maximize reproduction and survival of adults, and selection of nest microhabitat appears to have evolved in response to predation and microclimate (Walsberg 1981, Gloutney and Clark 1997). Nest microclimate can influence the energetic costs of incubation and the development and survival of eggs and young (Haftorn and Reinertsen 1985, Webb 1987). Many birds select nest microhabitats that ameliorate climatic factors and reduce physiological stress on adults, eggs, and young. Nest sites often are oriented nonrandomly relative to nearby objects or vegetation, presumably to accrue thermal benefits and protection from severe weather (Walsberg 1981, With and Webb 1993, Norment 1993). Birds that construct nests in cavities or with tunnel entrances frequently orient entrances relative to the solar path and prevailing winds (Facemire et al. 1990, Hooge et al. 1999, Wiebe 2001). Orientation of nests relative to surrounding vegetation also has been observed for relatively small-bodied open cup nesters, but large-bodied birds have received little attention (Walsberg 1981, Petersen and Best 1985, With and Webb 1993, Nelson and Martin 1999). Grasslands birds are exposed to wide daily and seasonal fluctuations in temperature, wind, and moisture, making nest microhabitat especially important. We studied nest microhabitat selection by dabbling ducks (Cinnamon Teal, *Anas cyanoptera*; Blue-winged Teal, *A. discors*; Gadwall, *A. strepera*; Mallard, *A. platyrhynchos*; and Northern Shoveler, *A. clypeata*) and Short-eared Owls (*Asio flammeus*). Specifically, we asked if orientation of nests relative to nearby vegetation differed from random. Based on patterns observed in our data, we also asked if a relative shift in orientation from southwest to northwest occurred with increasing nest initiation date.

METHODS

Study area.—We conducted research on 227 ha of ungrazed grassland habitat in the Mission Valley (47° 24′ N, 114° 24′ W), 80 km north of Missoula, Montana, during 1995–1997. Glacial topography characterizes the area, which exhibits low relief and high densities of wetlands (Lokemoen 1962). Vegetation was typical of habitat managed for upland-nesting ducks and Ring-necked Pheasants (*Phasianus colchicus*). Plant communities were structurally diverse, dominated by introduced cool season grasses, primarily intermediate wheatgrass (*Agropyron intermedium*), quackgrass (*A. repens*), smooth brome (*Bromus inermis*), Kentucky bluegrass (*Poa pratensis*), and orchard grass (*Dactylis glomerata*).

Field methods.—We commenced nest searching in late April and searched twice more at 21- to 25-day intervals using a cable chain device (Higgins et al. 1969). We monitored nests and estimated nest initiation dates following Klett et al. (1986). Observers could not always distinguish between female Cinna-

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TABLE 1. Candidate models examining support for orientation of nests and random locations relative to nearby vegetation and examining support for a seasonal shift in orientation for six species of ground-nesting grassland birds in westcentral Montana, 1995–1997.

Model set	Model[a]	Interpretation
Orientation	Constant	No support for orientation.
	Direction	Orientation by intercardinal direction, consistent across years.
	Direction × Year	Orientation by intercardinal direction, variable among years.
Shift	Constant	No support for shift.
	Initiation Date	Shift explained by individual response to nest initiation date.
	Median Initiation Date	Shift explained by interspecific differences in nesting phenologies.
	Initiation Date + Species	Shift explained by individual response to nest initiation date, but species differ in orientation for a given date.
	Initiation Date × Species	Shift varied among species.

[a] Models designated by sources of variation in data.

mon and Blue-winged teals, and we assumed that our sample of nests reflected the local predominance of breeding Cinnamon Teal (U.S. Fish and Wildlife Service, National Bison Range unpubl. data). These teal are closely related, physically similar (Johnson and Sorenson 1999), and likely selected similar nest sites. Therefore, we pooled these species (hereafter "teal") in analyses. We sampled vegetation when nests were no longer active, because we suspected that intensive sampling could increase nest abandonment and provide visual and olfactory cues that may increase nest predation. We assumed that rates of change in vegetation around each nest were similar and that relative differences at the time of sampling reflected patterns at the time of nest site selection. We used a 3.5 × 3.5-cm pole alternately marked black and white in 2-cm intervals (modified from Robel et al. 1970) to estimate an index of vegetation height and density (hereafter "vegetation"). From a height of 1 m and a distance of 4 m during 1995 and 2 m during 1996–1997, we recorded (in cm) the lowest visible interval. We shortened the observation distance because we thought that estimates taken from 2 m were more likely to be influenced only by vegetation near the pole. We made estimates while facing nests in the four intercardinal directions (NE, SE, SW, and NW) with the pole centered in the bowl; estimates were calibrated to ground level. We conducted identical sampling at random locations. We identified random locations from a grid superimposed on an aerial photo and then chose each sampling point by tossing a stick in a randomly selected direction. Nest orientation typically has been defined relative to a salient object (e.g., tunnel entrance or stem of nesting shrub) that describes aspect of exposure. Lacking a clearly defined reference object, we defined orientation as nest placement relative to vegetation immediately around nests.

Statistical analyses.—We modeled orientation at nests and random points using General Linear Models (SPSS, Inc. 2000). We used Akaike's Information Criterion corrected for sample size (AIC_c) to select parsimonious models for parameter estimation and inference (Burnham and Anderson 1998, Anderson et al. 2000). For each analysis, we created an *a priori* set of candidate models that mathematically represented different biological hypotheses concerning orientation; Akaike weights allowed us to assess relative support among these models. To assess the importance of individual variables, we summed Akaike weights for all models containing a variable.

To examine orientation, we modeled variation in the deviation of estimates of vegetation at each sampling point from the mean for that location. We considered the categorical predictive variables intercardinal direction (Direction) and year (Year). For each species and for random points, we created three *a priori* models to examine support for orientation (Table 1). To examine a perceived seasonal shift in relative vegetation from southwest to northwest, we modeled variation in the difference between estimates in these directions. We hypothesized that orientation shifted in response to seasonal northward change in the solar path and that a shift could result either from response of individuals or interspecific differences. A shift could occur if individuals, regardless of species, altered nest orientation in response to nest initiation date. Thus, we would predict that the individual covariate nest initiation date (Initiation Date) would best explain seasonal change in orientation. Alternatively, if individuals within a species did not alter nest orientation in response to initiation date, a shift could occur if each species selected orientation appropriate to its nesting phenology. Thus, we would predict that the group covariate of median nest initiation date for each species (Median Initiation Date) would best explain seasonal change in orientation. We developed five models to assess support for a shift and, if present, to attempt to distinguish if it was better explained by differences in orientation

TABLE 2. Selection results for models examining orientation of nests relative to nearby vegetation for six species of ground-nesting grassland birds and random locations during 1995–1997 in westcentral Montana. We present results for models with AIC_c weights >0.025.

Group	*n*	Model[a]	*K*[b]	log (*L*)[c]	ΔAIC_c[d]	AIC_c weight[e]
Teal[f]	168	Direction	5	−272.5	0.00	0.93
		Constant	2	−278.2	5.23	0.07
Gadwall	152	Direction	5	−262.9	0.00	0.67
		Constant	2	−266.8	1.42	0.33
Mallard	276	Direction	5	−513.2	0.00	0.54
		Constant	2	−516.5	0.34	0.46
Northern Shoveler	196	Direction	5	−245.1	0.00	0.99
Short-eared Owl	100	Direction	5	−167.3	0.00	0.98
Random	1244	Constant	2	−1,676.7	0.00	0.63
		Direction	5	−1,674.2	1.05	0.37

[a] Models designated by source(s) of variation in vegetation immediately around nests.
[b] Number of estimated parameters.
[c] Maximized log-likelihood.
[d] Difference in AIC_c relative to model with lowest value for each group.
[e] Weight of evidence for being the best approximating model for each group.
[f] Cinnamon and Blue-winged teals pooled.

among species or responses of individuals regardless of species (Table 1). We also considered the categorical predictor species (Species) to estimate potential differences in orientation among species after controlling for a seasonal shift. To assess support for a seasonal shift in orientation at random locations, we considered a constant model versus a model with the continuous covariate date (Date).

RESULTS

Nest orientation.—We included 225 nests in our analyses: 42 teal, 40 Gadwall, 69 Mallard, 49 Northern Shoveler, and 25 Short-eared Owl. Sixty-eight nests were from 1995, 86 from 1996, and 71 from 1997. The Direction model was selected as the best approximating model of orientation for each species (Table 2). Strong support for the Direction model existed for three species (AIC_c weights were >13× those for the next best model). Only moderate support existed for Mallards and Gadwalls (AIC_c weights 1.2–2.0 those for the next best model), but patterns in estimates and effects were similar for all ducks. Vegetation to the southeast of nests was relatively low for all species. Species nesting relatively early (Mallard, Northern Shoveler, and Short-eared Owl) had relatively high vegetation to the southwest of nests, but species nesting relatively late (Gadwall and teal) had relatively high vegetation to the northwest (Fig. 1). For each species, the 95% CI for the difference between directions with highest and lowest estimates did not include zero. For random points, the Constant model received moderately more support (AIC_c weight 1.7×) than the Direction model (Table 2). Although the Direction model received some support, estimated differences in vegetation among directions from this model were small, and 95% CI's for all estimates overlapped zero (Fig. 1). Direction × Year models received virtually no support (AIC_c weights <0.025).

Seasonal shift in orientation.—Among models examining a seasonal shift in orientation, two models including Initiation Date received similar support as the best approximating model (Table 3). These models received >3× more support than a model including Median Initiation Date, and other models received little support. Summed Akaike weights for models including individual variables provided >6× more support for the predictive importance of Initiation Date (0.85) relative to Median Initiation Date (0.13), indicating that a seasonal shift in orientation was best explained by individual response to nest initiation date. The top model predicted that vegetation to the southwest relative to the northwest of nests decreased ($\beta_1 = -0.128$; 95% CI −0.047, −0.209; $n = 225$) as estimated nest initiation date increased (Fig. 2). The predicted shift in mean vegetation was 10.6 cm across the range of nest initiation dates, and the combined mean for both directions was 24.6 cm. Thus, nearly half (43%) of

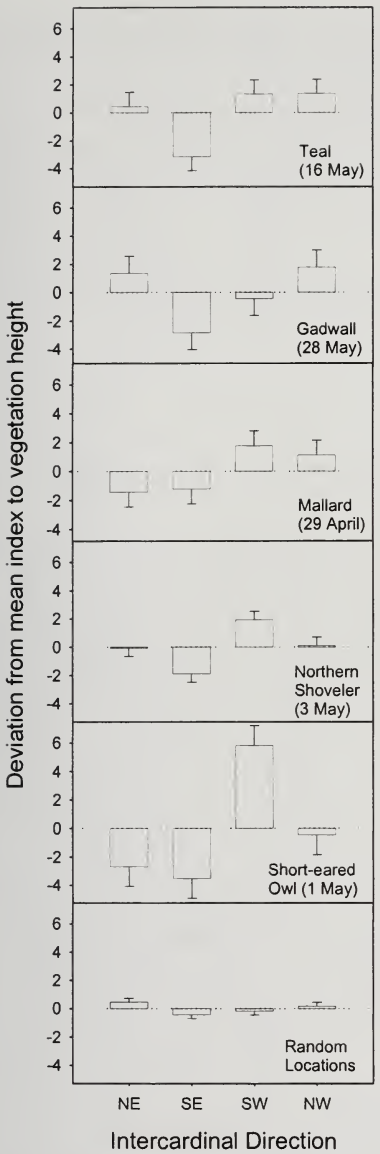

FIG. 1. Deviations (+1 SE) in an index of vegetation height and density in intercardinal directions relative to the mean for that location for nests of six species of ground-nesting grassland birds (median initiation date) and random locations during 1995–1997 in westcentral Montana. Reference lines indicate no difference from mean.

the total vegetation was predicted to shift direction, suggesting that the magnitude of the estimated effect was biologically important. The second best model predicted a more moderate effect of estimated initiation date (β_1 = −0.083; 95% CI 0.016, −0.181), and differences in vegetation between southwest versus northwest were predicted to be greater by about 5 cm for Short-eared Owls relative to ducks. In contrast to patterns at nests, support for a seasonal shift at random locations was equivocal (Table 3). The relatively small slope from the Date model (β_1 = −0.031; 95% CI 0.009, −0.070; n = 616) could not account for patterns at nests.

DISCUSSION

Microclimate is thought to be an important determinant of nest microhabitat selection for small birds (Walsberg 1985), because they are relatively susceptible to thermal stress. Many small birds appear to orient nest sites to gain thermal benefits (Walsberg 1981, With and Webb 1993, Nelson and Martin 1999). Explanations of nest orientation have focused primarily on optimization of thermal microclimate relative to solar insolation and convective cooling, the major sources of heat exchange at nests (Webb and King 1983). Birds nesting in cool or hot environments may increase or decrease exposure to the sun (Inouye et al. 1981, Finch 1983, Petersen and Best 1985), and birds exposed to wide daily variation in temperature may moderate thermal variation by increasing heat gain in the morning but decreasing it in the afternoon (Walsberg 1981, With and Webb 1993, Hooge et al. 1999, Nelson and Martin 1999). Alternatively, birds may orient nests relative to the prevailing wind to facilitate convective cooling or to reduce exposure to weather (Facemire et al. 1990, Viñuela and Sunyer 1992, Norment 1993).

We believe that support for nest orientation in this study was novel for large-bodied grassland birds, and we suggest that nest sites were selected in part to ameliorate nest microclimate. Consistent patterns of orientation across species suggested common thermal benefits to nest microclimate. The pattern of least vegetation to the southeast and most to the southwest or northwest of nests suggested that birds selected sites that were relatively exposed in the morning to maximize heat gain but shaded in the afternoon to avoid excessive insolation. Energetic costs of incubation increase as ambient temperature declines below a lower critical temperature (T_{lc}; Haftorn and Reinertsen 1985). Assuming body temperatures of 40° C

TABLE 3. Selection results for models examining seasonal shift in relative vegetation immediately to the southwest versus northwest of nests of six species of ground-nesting grassland birds and random locations during 1995–1997 in westcentral Montana. We present results for models with AIC_c weights >0.02.

Group	Model[a]	K[b]	log ($\mathcal{L}$)[c]	ΔAIC_c[d]	AIC_c weight[e]
Nest	Initiation Date	3	−458.8	0.00	0.45
	Initiation Date + Species	6	−455.7	0.23	0.40
	Median Initiation Date	3	−460.0	2.51	0.13
Random	Date	3	−1,173.0	0.00	0.50
	Constant	2	−1,174.0	<0.01	0.50

[a] Models designated by source(s) of variation in difference (southwest − northwest) of vegetation immediately around nests.
[b] Number of estimated parameters.
[c] Maximized log-likelihood.
[d] Difference in AIC_c relative to model with the lowest value for each group.
[e] Weight of evidence for being the best approximating model for each group.

and typical masses for breeding females, estimated T_{lc} for our study species ranged between about 10° C for Mallards to about 16° C for teal (Calder and King 1974: equation 20). Ambient temperatures on our study area early in the nesting season or at night typically were below T_{lc} of females. Similarly, temperatures at nests of Mallards and Blue-winged Teal have been demonstrated to be below their T_{lc} for most of the night (Gloutney and Clark 1997). Selecting nests with relatively high southeast exposure likely facilitated heat gain during the morning (Nelson and Martin 1999) and thereby reduced energetic costs of incubation.

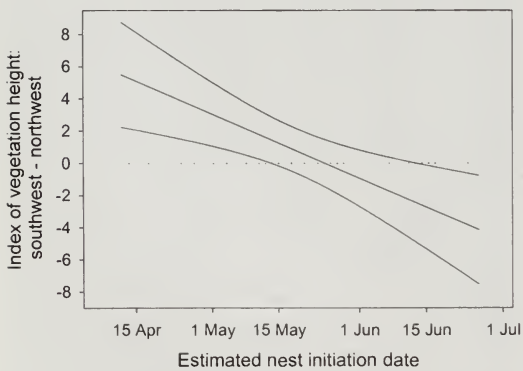

FIG. 2. Difference between an index of vegetation height and density immediately to the southwest and the northwest of nests of dabbling ducks (Cinnamon Teal, *Anas cyanoptera*; Blue-winged Teal, *A. discors*; Gadwall, *A. strepera*; Mallard, *A. platyrhynchos*; and Northern Shoveler, *A. clypeata*) and Short-eared Owls (*Asio flammeus*) relative to estimated nest initiation date during 1995–1997 in westcentral Montana, with 95% CI for predicted mean values. Positive values indicate more vegetation to the southwest relative to the northwest; dotted line indicates no change over time.

In contrast, ambient temperatures in the afternoon often reached 35°C, and ground temperatures likely reached levels causing stress to nesting females and reducing growth and survival of eggs and young (Webb 1987, Nelson and Martin 1999, Conway and Martin 2000). Nesting ducks typically take incubation recesses during early afternoon (Gloutney et al. 1993). Unattended eggs can reach deleterious temperatures rapidly when exposed to insolation (White and Kinney 1974, Bennett and Dawson 1979), suggesting that increased shading from afternoon insolation may be important for moderating egg temperature.

Gloutney and Clark (1997) found that Mallards and Blue-winged Teal selected nest sites shaded from intense insolation during afternoon hours, and patterns we observed were consistent with that observation. Support for a shift from southwest to northwest in vegetation near nests with increasing nest initiation dates suggested that individual females tracked seasonal changes in the solar path when selecting nest sites. When nesting began in early April, the sun was in the southern hemisphere of the sky for most of the day. However, the sun was near its northernmost extent from late May to the end of July, spending nearly half of the afternoon in the northern hemisphere of the sky and setting to the northwest. Others have observed relatively abrupt seasonal switches from nest orientations increasing to those decreasing heat gain as ambient temperatures increased (Austin 1976, Finch 1983). However, we believe that

our interpretation of a relatively subtle change in orientation to maintain shading in response to seasonal change in the solar path is novel.

Alternatively, relatively greater vegetation to the southwest and northwest may have provided protection and reduced convective heat loss at nests from prevailing winds from the west-northwest (National Oceanic and Atmospheric Administration unpubl. data). However, the shift in orientation through the breeding season was more consistent with the hypothesis that shading was primary to orientation. Gloutney and Clark (1997) reported only limited selection by Mallards and Blue-winged Teal to ameliorate climatic factors at nests and suggested that microclimate may have little influence on site selection in ducks. However, effects of orientation may not have been detected because microclimate was measured >10 cm outside the center of nests (orientation unspecified). In our study, birds oriented nests relative to small bunches of grass, and microclimate benefits likely did not extend much beyond the nest bowl.

Selection of habitat type also may ameliorate microclimate. Ducks nesting in relatively tall, uniform cover (e.g., the parkland habitat in Gloutney and Clark 1997) may have little need or even opportunity to orient nests, and fine scale differences in microhabitat and microclimate may be small within suitable nesting habitat. In relatively sparse and heterogeneous vegetation (e.g., sites dominated by bunchgrasses, grazed sites), fine scale variation in microhabitat and hence microclimate may constrain suitable nest sites.

The orientation that we observed was unlikely to have been an artifact of vegetation bent over by prevailing winds from the west-northwest, as no comparable differences occurred at random locations. Alternatively, nests under blown down vegetation may have been selected for overhead cover rather than orientation *per se.* However, Mallards and teal nested almost exclusively in bunchgrasses with stiff stems and leaves that were not prone to blowing over; in addition, Short-eared Owls selected for almost no overhead cover (STH unpubl. data) but showed the strongest orientation of vegetation around nests.

Ultimately, birds should select nest sites that minimize reproductive failure and hence maximize fitness. Nests that deviate from the typical orientation at a site often experience decreased reproductive success (Austin 1976, Högstedt 1978, Viñuela and Sunyer 1992, Hooge et al. 1999, Wiebe 2001). Predation is the primary cause of nest failure in most birds (Martin 1993). Most studies of nest microhabitat selection by grassland birds have focused on the relationship between concealment and predation, thereby tacitly assuming that microhabitat selection responds primarily to predation pressure (Clark and Nudds 1991, DeLong et al. 1995). Unsuitable nest microclimates could increase energetic needs of adults and hence decrease nest attentiveness, which could prolong exposure to predation (White and Kinney 1974, Webb 1987, Yanes et al. 1996, Loos 1999) or increase vulnerability of nests to predators (Högstedt 1978, Martin et al. 2000a, 2000b). Further study of selection of nest microhabitat in grasslands will be needed to determine consequences for nest microclimate, parental energetics and behavior, and reproductive success.

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HABITAT ASSOCIATIONS OF MEXICAN SPOTTED OWL NEST AND ROOST SITES IN CENTRAL ARIZONA

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ABSTRACT.—We analyzed landscape characteristics surrounding Mexican Spotted Owl (*Strix occidentalis lucida*) nest and roost trees in Arizona at three spatial scales: one circular plot of 201 ha (800-m radius) and two 400-m-wide "ring" plots between 800 m and 1,600 m from each nest or roost tree. The percentages of vegetation types were significantly different between 51 owl and 51 random areas only within the 201-ha circular plots. Owls selected both mature and young mixed conifer forests that had high canopy closure (≥55%) more than expected based on availability. Owls selected pine (*Pinus* spp.) and pine-oak (*Quercus* spp.) forests in proportion to availability. Forty-one percent of all nests and roosts were located in mixed conifer forests, even though this forest type covered only 5% of the study area. Pine and pine-oak forests covered 78% of the study area, and 59% of nests and roosts were located in these forest types. The only forest type in which we did not locate nests and roosts was mature open canopy ponderosa pine (*P. ponderosa*) forest. Owls occupied areas of predominantly younger forests, but only if residual large (≥45.7 cm dbh) trees were present. Indices of landscape structure did not differ significantly between owl and random areas. Future management of Mexican Spotted Owls in areas of moderate topographic relief should focus on retention of mature forests, especially mixed conifer stands with canopy closure ≥55%. Residual large trees, especially Gambel oaks (*Q. gambelii*), are important microhabitat components in younger forests. *Received 19 February 2002, accepted 4 November 2002.*

The association between Spotted Owls (*Strix occidentalis*) and late seral stage forests has been documented for both the Northern (*S. o. caurina*) and California (*S. o. occidentalis*) subspecies (Gutiérrez et al. 1995). The habitat associations of the Mexican Spotted Owl (*S. o. lucida*) led in part to the listing of the subspecies (U.S. Dept. of Interior 1993, 1995), even though these associations were not understood as clearly as for the threatened Northern Spotted Owl (U.S. Dept. of Interior 1990). Limited evidence has suggested that Mexican Spotted Owls may not depend upon old growth forests to the same degree as the Northern and California Spotted Owls (Ganey and Balda 1989a, Seamans and Gutiérrez 1995).

Past research into the habitat requirements of Mexican Spotted Owls has included analysis of fine scale (≥0.2 ha) habitat selection (see review by Ganey and Dick 1995) and landscape scale (≥201 ha) habitat selection (Ganey and Balda 1994, Grubb et al. 1997, Ganey et al. 1999, Peery et al. 1999). These studies found that owls occupy mature forests with dense canopy cover. However, most of these previous studies were conducted in areas of mixed conifer forest and steep terrain. The Mexican Spotted Owl occupies a variety of environments in the Southwest, including mixed conifer forest, pine (*Pinus* spp.)-oak (*Quercus* spp.) forest, and canyons (Ward et al. 1995). We studied a Mexican Spotted Owl population occupying an area of moderate topography dominated by pine-oak forest. Therefore, our study broadens the understanding of habitat selection by Spotted Owls in the southwestern United States.

Data on the spatial configuration (e.g., fragmentation) of vegetation types around Mexican Spotted Owl nest and roost sites have been limited (Ganey and Dick 1995). Peery et al. (1999) found no difference in the spatial configuration of vegetation types between Mexican Spotted Owl sites and random sites in an area of steep terrain and mixed conifer forest in New Mexico. For the two coastal subspecies, some studies have reported Spotted Owls in areas less fragmented than the surrounding landscape (Hunter et al. 1995, Moen and Gutiérrez 1997) while other studies have found no difference between owl and random sites (Carey et al. 1992, Ripple et al. 1997). Therefore, we examined the spatial configuration of vegetation types around Mexican Spotted Owl nest and roost areas to estimate the utility of landscape metrics for dis-

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tinguishing Spotted Owl habitat on our study area.

The objective of our research was to estimate landscape scale habitat selection by Mexican Spotted Owls in northcentral Arizona. In particular, we predicted (1) landscapes around Spotted Owl nest and roost sites would contain more mature, closed canopy forest than landscapes around random sites, and (2) the spatial pattern of vegetation types in landscapes around Spotted Owl nest and roost sites would be less fragmented than the pattern of vegetation types in landscapes around random sites.

METHODS

Study area.—Our study area encompassed 585 km^2 of the Coconino National Forest (34° 51′ N, 111° 28′ W) and was located 40 km southeast of Flagstaff, Arizona. Primary land uses were timber harvesting, livestock grazing, and recreation. Selection harvest was the dominant timber management technique. The topography was gentle with several small cinder cones throughout the area; elevations ranged from 1,800 to 2,660 m.

Three major forest communities occurred within the study area. Mixed conifer forest was dominated by Douglas-fir (*Psuedotsuga menziesii*) and white fir (*Abies concolor*) with subdominant ponderosa pine (*Pinus ponderosa*), quaking aspen (*Populus tremuloides*), and Gambel oak (*Quercus gambelii*). Mixed conifer forest was present at higher elevations and on north-facing slopes. Pine-oak forest was dominated by ponderosa pine and Gambel oak, and was present at mid-elevations and on south-facing slopes. Lower elevations consisted of piñon-juniper woodland dominated by piñon pine (*Pinus edulis*) and junipers (*Juniperus deppeana* and *J. monosperma*).

The climate within the study area was characterized by cold winters (mean maximum daily temperature = 6° C) and warm summers (mean maximum daily temperature = 25° C). Precipitation occurred primarily from December through March in the form of snow; however, monsoon thundershowers were common from mid-July through September.

Owl and random locations.—We used standard Spotted Owl surveying techniques (Forsman 1983, Franklin et al. 1996) to locate nest and roost trees from April to August (i.e., breeding season) of each year. We attempted to capture all owls detected on the study area. We marked each captured owl with a numbered, locking aluminum leg band and a colored leg band on opposite legs. We used the colored leg bands (see Forsman 1983, Franklin et al. 1996) to identify individual owls and to assign individuals to unique territories.

We randomly selected one nest or roost tree per territory from among all those found from 1991 through 1996. By selecting one tree per territory we maintained sampling independence and obtained a location for centering owl sample plots in each territory. We established *a priori* an order of selection to reflect a continuum of stronger to weaker association with the activity center of a given territory. Our order of selection was (1) nest tree, (2) pair roost, (3) male roost. Therefore, we used a nest tree if one was available; otherwise, we selected a roost tree. Hereafter, nest and roost plots will be referred to as owl areas.

Using IDRISI 4.1 (Eastman 1994), we located a random set of comparison areas by generating random Universal Transverse Mercator (UTM) coordinates within the study area. We excluded locations that fell in water or large grassland areas. To maintain sampling independence, each random point was ≥2,400 m from any other random point. This distance represented the mean nearest neighbor distance between owl territory centers (n = 42) during 1993, the year of highest density. Hereafter, these random locations will be referred to as random areas.

We used a Trimble GeoExplorer™ global positioning system to record the center of owl and random areas accurately. We conducted differential correction of all locations using base station data from either the Coconino National Forest Supervisor Office or USGS Colorado Plateau Research Station, both located in Flagstaff, Arizona.

Classification of vegetation types.—We used a Landsat 5 Thematic Mapper-based vegetation map developed by D. W. Farris (unpubl.). The initial Landsat image was taken on 14 June 1994 and included a buffer zone around the study area to allow analysis of owl and random areas whose centers fell close to the study area boundary. We conducted *a priori* vegetation sampling and iteratively verified map classification until image accuracy was ≥75% (May 2000).

We assessed the final accuracy of the map by first selecting a set of random UTM points. We then located each point in the field and assigned the surrounding area to a vegetation classification based on dominant species composition, dbh size classes, and canopy closure of trees (see Appendix). We used a wedge prism of 10 basal area factor to estimate trees in a variable radius plot (Dilworth 1981) centered at each UTM location. For each tree within the plot, we recorded species and dbh. We defined mature trees as those ≥45.7 cm dbh. We used a concave spherical densiometer to estimate canopy closure within each plot by calculating the mean of the measurements taken at each of the major compass directions at a distance of 10 m from the plot center. We defined areas ≥55% overhead cover as closed canopy. Finally, we compared the vegetation type assigned in the field to the predominant vegetation class within the 90- × 90-m corresponding area of the final Landsat map. We expressed accuracy as a percentage of agreement between field and image plots.

Analysis of vegetation types.—We used IDRISI 4.1 to delineate three concentric, nonoverlapping plots around each owl nest or roost tree and each random UTM location. The smallest plot was 201 ha (i.e., 800-m radius circle). The other two areas were 400-m-wide

"ring" plots (see Swindle et al. 1999) measuring 1,200 m and 1,600 m to the outer edges. Previous studies found that areas of 201 ha may have an important influence on Spotted Owl habitat selection for nest and roost sites (Grubb et al. 1997, Meyer et al. 1998, and Swindle et al. 1999). The intermediate plot size corresponded to the mean nearest neighbor distance between owl territory centers on our study area during the year of highest density. The largest plot size represented the mean home range size of paired Mexican Spotted Owls (Ganey and Balda 1989b).

We measured characteristics of vegetation types using IDRISI 4.1 and FRAGSTATS 2.0 (McGarigal and Marks 1995). We used owl areas to estimate Spotted Owl habitat selection while random areas represented available habitat in the landscape. Between owl and random areas, we compared (1) the percentages of vegetation types within plots; and (2) the landscape pattern measured by mean patch size (ha), mean patch shape index, and contagion of patches (Li and Reynolds 1993). We set the minimum patch size equal to the image resolution (i.e., 30 × 30 m). We analyzed landscape pattern only within the 201-ha plots. We did not analyze landscape pattern within the ring plots because we felt the variables would be most meaningful when measured within a relatively uninterrupted landscape (i.e., one in which potential edge effects were minimized).

Li and Reynolds (1994) found that indices of landscape pattern were autocorrelated and quantified slightly different aspects of overall pattern (i.e., they were not independent). However, Riitters et al. (1995) found that two of the indices we chose, mean patch shape index and contagion, were independent based on principal component analysis of 85 maps representing various landscape patterns and physiographic regions. Therefore, we felt the indices we chose provided relatively independent assessments of landscape pattern between owl and random areas.

If owls are associated with extensive areas of a particular vegetation type, owl areas should have lower values for mean patch shape index while mean patch size and contagion should be greater. Because mean patch shape is a measure of the complexity of all patches in an area using a perimeter-to-area ratio, a lower value for owl areas suggests that owls are selecting habitat containing large core areas for nesting and roosting. Contagion is a measure of both distribution and degree of intermixing of vegetation types in a landscape and expresses the probability that two adjacent pixels (i.e., image cells) belong to the same vegetation type. Thus, a higher value of this metric for owl areas suggests that owls select landscapes containing clumps of similar habitat.

Data analysis.—The data used for these analyses were nonnormal and heteroscedastic. Therefore, we used the multiresponse permutation procedure (MRPP) of program BLOSSOM (Cade and Richards 2001) for all analyses. MRPP is a distribution free test analogous to ANOVA. MRPP uses permutations of the data from randomization theory to provide probabilities of type I error (Edgington 1987). We used a multivariate MRPP test to examine differences in all vegetation types collectively at each plot size. Where significant differences occurred, we used univariate MRPP tests to determine which vegetation type(s) were responsible for the differences. For landscape pattern comparisons, we used only univariate MRPP tests. Due to the nonnormality of the data, we present differences as medians with 25% and 75% quantiles. To avoid type I error, we adjusted the significance level for multiple comparisons using the formula ($P < 0.05/k$), where k was the number of variables tested.

Post hoc description of microhabitat characteristics in young forests.—Our analysis of landscape scale plots indicated that Mexican Spotted Owls selected areas containing young mixed conifer forest. Because this finding seemed contrary to previous Spotted Owl research, which has shown an association of owls with mature and old growth forests, we examined microhabitat characteristics around owl nest and roost trees in all types of young forest. We collected data within 0.04 ha surrounding owl nest and roost trees according to methods described by Seamans and Gutiérrez (1995). We summarized the occurrence of cavity nests and mature trees in these plots.

RESULTS

Classification of vegetation types.—We classified eight vegetation types (see Appendix) with a final map accuracy of 80% (n = 88 random plots) within the study area and 81% (n = 123 random plots) within the study area and its buffer zone combined. Errors were limited primarily to mature open canopy ponderosa pine forest being misclassified as young forests of ponderosa pine and ponderosa pine-Gambel oak. Because young forests of ponderosa pine and ponderosa pine-Gambel oak (see Appendix for vegetation type descriptions) represented owl habitat (i.e., contained nests and roosts) but mature open canopy ponderosa pine forest was not owl habitat, we did not combine these vegetation types further.

Owl and random locations.—From 1991 through 1996, we located 84 different nest trees and 193 different roost trees in 51 unique owl territories. We used 31 nests, 16 pair roosts, and 4 male roosts in our analysis. Density was 0.147 territorial owls/km^2 during 1993, the year of highest owl density. However, we found owl nests and roosts in only five of the eight vegetation types (Fig. 1). Therefore, the ecological density (density in the five vegetation types where we located

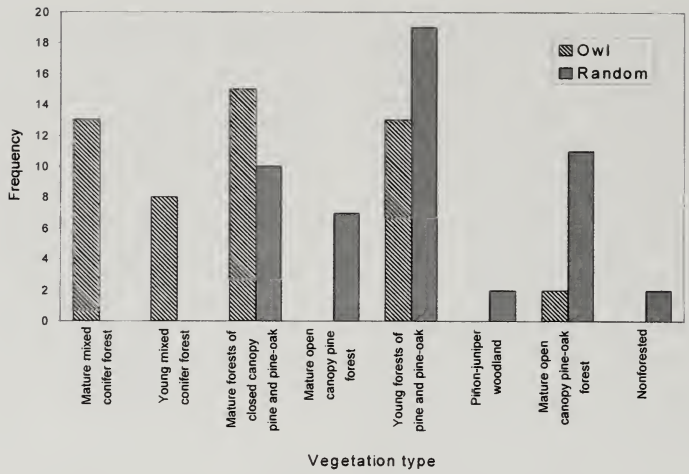

FIG. 1. Mexican Spotted Owls used mixed conifer forests for nesting and roosting more frequently than expected when compared to random locations on the Mexican Spotted Owl study area, central Arizona, 1991–1996. Owls used other vegetation types in proportion to availability.

nests or roosts; Tanner 1978) was 0.212 territorial owls/km^2 during 1993.

Analysis of vegetation types.—The percentages of vegetation types differed between owl areas and random areas only within 201 ha surrounding plot centers (multivariate MRPP, $P < 0.0001$). Univariate tests indicated that mature mixed conifer forest and young mixed conifer forest were responsible for differences, suggesting that owls selected landscapes containing these forest types. Canopy closure in both mixed conifer forest types was ≥55%. Owl areas contained a higher percentage of mature mixed conifer forest at the 201-ha scale than random areas (owl: median = 3.5%, 25% quantile = 0.6%, 75% quantile = 12.1%; random: median = 0.2%, 25% quantile = 0%, 75% quantile = 1.2%; univariate MRPP, $P = 0.0005$; Table 1). Owl areas contained a higher percentage of young mixed conifer forest at the 201-ha scale than random areas (owl: median = 1.5%, 25% quantile = 0%, 75% quantile = 10.3%; random: median = 0.2%, 25% quantile = 0%, 75% quantile = 1.3%; univariate MRPP, $P = 0.0002$; Table 1). The percentages of other vegetation types

TABLE 1. Landscapes within 201 ha (800-m radius circle) around 51 Mexican Spotted Owl nest and roost sites contained significantly higher median percentages of mature and young mixed conifer forests than landscapes around 51 random sites in central Arizona. Landscapes contained other vegetation types in proportion to availability.

	Owl			Random		
		Quantiles			Quantiles	
Vegetation type	Median	25%	75%	Median	25%	75%
Mature mixed conifer forest*	3.5	0.6	12.1	0.2	0.0	1.2
Young mixed conifer forest*	1.5	0.0	10.3	0.2	0.0	1.3
Mature closed canopy forests of ponderosa pine and ponderosa pine-Gambel oak	17.9	9.9	26.0	12.9	5.7	23.5
Mature open canopy ponderosa pine forest	4.9	2.3	11.5	11.5	6.1	18.7
Young forests of ponderosa pine and ponderosa pine-Gambel oak	41.5	31.6	50.7	39.5	32.0	51.5
Piñon pine-juniper woodland	0.0	0.0	0.2	0.1	0.0	1.2
Mature open canopy ponderosa pine-Gambel oak forest	7.5	3.7	10.3	10.4	4.9	17.5
Nonforested	5.5	2.5	9.8	11.3	5.3	19.8

* Owl areas and random areas differed significantly at $P \leq 0.0005$.

within 201 ha of plot centers did not differ significantly (range of *P*, 0.008–0.75), suggesting landscapes around owl areas contained these vegetation types in proportion to availability. Multivariate analysis of the vegetation types within the two sets of ring plots indicated there was no significant difference between owl areas and random areas (MRPP, 1,200 m ring: $P = 0.06$, 1,600 m ring: $P = 0.10$).

Landscape pattern indices within 201 ha of plot centers did not differ significantly between owl and random areas (mean patch size: owl = 1.67, random = 1.55, MRPP $P = 0.19$; mean patch shape index: owl = 1.38, random = 1.36, MRPP $P = 0.61$; contagion: owl = 39.10, random = 38.69, MRPP $P = 0.32$). The statistical power of these tests was low (0.24, 0.33, and 0.06 for mean patch size, mean patch shape index, and contagion, respectively). While we acknowledge the limited use of retrospective power analysis (Thomas 1997), we examined the effect sizes necessary to produce significant results. Given our sample size and observed variances (depending on the landscape index considered), the effect sizes would had to have been 2 to 12 times the observed values to increase power to 0.80. Alternatively, power could be increased by increasing the sample size. However, given the observed data and the density of Spotted Owl territories in the area, a study area would have to encompass 1,900–79,000 km^2 to provide significant results.

Description of microhabitat characteristics in young forests.—We located 21 (41%) nest and roost trees in young mixed conifer forest or young forests of ponderosa pine and ponderosa pine-Gambel oak (Fig. 1). Of the eight nests and roosts located in young mixed conifer stands, six had the same or higher percentages of mature mixed conifer forest (median = 20.1%) than young mixed conifer forest (median = 15.0%) within the 201-ha plots. Furthermore, the five owl pairs that nested in young mixed conifer stands chose cavities in mature trees. Hence, we would describe young mixed conifer stands used by owls as young stands with residual large trees. Overall, we located 21 (41%) owl nests and roosts in young and mature mixed conifer forest types.

We found 13 (25%) nest and roost trees in young forests of ponderosa pine and ponderosa pine-Gambel oak (Fig. 1). However, this forest type also contained residual mature or old growth trees not detected during image classification. Of the seven nests located in such forests, all were in cavities of mature Gambel oaks. In addition, five of six (83%) roost stands contained mature trees within a 0.04-ha area around roost trees. Overall, we located 30 (59%) owl nests and roosts in pine or pine-oak forest types.

DISCUSSION

Habitat selection.—Spotted Owls on the study area selected landscapes containing both mature and young mixed conifer forests within 201 ha of nest and roost trees. These mixed conifer forests were characterized by canopy closures ≥55% and, for mature forest, large trees. In areas of young forest, owls used stands with residual large trees in the immediate vicinity of nests and roosts. Mexican Spotted Owl selection of landscapes containing mixed conifer forests and dense canopy cover conditions has been documented previously (see review in Ganey and Dick 1995, Grubb et al. 1997, Peery et al. 1999); however, its relative importance was not demonstrated so clearly as in this study. Mixed conifer forest comprised <5% of our study area, yet 63% of owl areas (201 ha plots) contained such forest.

With the exception of mature open canopy ponderosa pine forest, Mexican Spotted Owls on our study area selected ponderosa pine forests and ponderosa pine-Gambel oak forests in proportion to availability. As with mixed conifer forest, residual large trees in younger forests appeared to be an important microhabitat component for nesting and roosting. Ganey et al. (1999) reported similar results from an area without mixed conifer forest. In addition, they found owls used areas of relatively high canopy closure and suggested that large trees were more important than dense stands of small trees (Ganey et al. 1999).

California and Northern Spotted Owls also nest and roost in young forests that contain residual large trees (Bias and Gutiérrez 1992, Folliard et al. 1993, Moen and Gutiérrez 1997, LaHaye and Gutiérrez 1999). In addition, Thome et al. (1999) found more residual large trees in the territories of Northern Spotted

Owls having high reproductive success than in owl territories having low reproductive success. The use of younger forests with residual large trees may be a case of proximate factors in the environment eliciting a settling response (Hildén 1965). Specifically, the presence of a suitable nest site or variability in alternative roost sites (i.e., to avoid weather or climate fluctuations), both of which residual large trees provide, may be a sufficient cue to elicit settling by Spotted Owls in the Southwest. However, the detection of residual large trees has proven to be difficult in Landsat analysis of Spotted Owl habitat (e.g., Moen and Gutiérrez 1997, this study).

The importance of closed canopy forests to Spotted Owl habitat selection at the landscape scale is unknown. Several hypotheses have been proposed for the selection of closed canopy stands by Spotted Owls at smaller scales; these hypotheses include favorable microclimate conditions (see review in Ganey and Dick 1995), protection from predators (Ganey et al. 1997), and more abundant prey (Gutiérrez 1985, Carey et al. 1992). Ganey and Dick (1995) suggested that evidence favors the microclimate hypothesis for Mexican Spotted Owl selection of nesting and roosting habitat. The data required to evaluate the relative importance of these hypotheses at the landscape scale are limited. However, Svärdson (1949) suggested that a bird may select a territory when the sum of external stimuli reaches a critical threshold level. Therefore, the multiple environmental cues implied in the different hypotheses may combine in different ways to elicit innate settling responses in different Spotted Owls. It also is possible that the occurrence of closed canopy forests at the landscape scale is simply a result of landscape pattern (e.g., clumping of closed canopy forest patches) and coincidental with selection by Spotted Owls at a smaller scale.

Other studies found close associations between Mexican Spotted Owls and old growth mixed conifer and pine forests in the southwestern United States (Ganey and Balda 1994, Zwank et al. 1994, Peery et al. 1999). However, the percentage of old growth and mature forest at owl sites in our study was less than in the above studies. Previous researchers found 42–56% of Mexican Spotted Owl home ranges or territories were in mixed conifer forest, compared to 15% in our study (Ganey and Balda 1994, Zwank et al. 1994, Peery et al. 1999). In addition, we recorded lower amounts of old growth and mature forest within owl areas than reported in the Pacific Northwest (76.3%, Ripple et al. 1991; 58%, Carey et al. 1992; 43.5%, Hunter et al. 1995). Therefore, our results suggested that either Spotted Owls on the study area are not old forest dependent *per se* or they are living in lower quality habitat.

While Spotted Owls on our study area appear to rely less on mature forests of mixed conifer and pine-oak compared to Spotted Owls in other parts of their range, the population on our study area experiences relatively large ($\bar{x}$ = 23%) annual fluctuations (RJG unpubl. data). The amplitude of these fluctuations could be the result of lower quality habitat available for nesting, roosting, and foraging. Further, we do not know the relative fitness potential (*sensu* Franklin et al. 2000) of these young forests. In addition, our highest ecological density (0.212 owls/km^2) was lower than most other Spotted Owl populations. Ecological density was estimated to be 0.48 owls/km^2 for Mexican Spotted Owls (Rinkevich and Gutiérrez 1996), 0.139 owls/km^2 (Bias and Gutiérrez 1992) to 0.40 owls/km^2 (Smith 1995) for California Spotted Owls, and 0.544 owls/km^2 for Northern Spotted Owls (Franklin et al. 1990). All these studies used comparable methods, therefore, direct comparisons are appropriate.

Several studies of the two coastal Spotted Owl subspecies have reported that owl sites have less forest fragmentation than random sites (Lehmkuhl and Raphael 1993, Hunter et al. 1995, Moen and Gutiérrez 1997, Meyer et al. 1998). However, we did not find differences in landscape indices between owl and random areas. This could be due to (1) the scale we chose to conduct the analysis, (2) the difficulty in quantifying landscape pattern (Morrison et al. 1992), (3) the actual absence of a strong difference, or (4) the autocorrelation between the area of vegetation types and landscape parameters (Li and Reynolds 1994). However, at least three other studies found landscape indices of little or no use in predicting Spotted Owl habitat selection (Carey et al. 1992, Ripple et al. 1997, Peery et al. 1999).

Our results support other research that has found the area within 800 m of Spotted Owl nest and roost trees may have the greatest influence on habitat selection (Grubb et al. 1997, Meyer et al. 1998, Swindle et al. 1999). Mean home range size for Spotted Owls near our study area is about 900 ha, or the area within about 1,700-m radius of a nest or roost tree (Ganey and Balda 1989b, Ganey et al. 1999). We did not find evidence of Spotted Owl selection for specific vegetation types beyond 800 m from nest and roost trees. However, Mexican Spotted Owls do use larger areas for foraging (Ganey and Dick 1995, Ganey et al. 1999).

Management implications.—In this breeding season study, Spotted Owls showed the strongest association with closed canopy mixed conifer forests. Although only 4.8% of the study area consisted of mixed conifer forest, 56% of this forest type was contained within 51 201-ha owl areas. Therefore, future management for this species in our study area should strive for the retention of mixed conifer forest for nesting and roosting. In addition, we recommend younger forests be managed for the development or retention of large trees.

The median area of mature closed canopy forest in the 201-ha owl areas was 55 ha; however, this does not indicate a minimum area for protection around owl nests and roosts. Given the amplitude of population fluctuations and relatively low ecological density, protected areas probably should contain more mature forest. Although owls selected most pine and pine-oak forests in proportion to availability, we do not know if the species can persist in these habitats. Additional research will be required to address the relationship between Spotted Owl demographic parameters and habitat quality.

The use of ecological restoration techniques for forest management has received much attention. Such restoration in the southwestern United States involves reductions in basal area of trees, tree density, and canopy cover to return land to presettlement conditions (Covington and Moore 1994, Covington et al. 1997). Ideally, these management practices would produce forests similar to the mature open canopy ponderosa pine forest of this study, the only forest type in which we did not locate any Spotted Owl nest or roost trees. However, it is not clear whether forest structure in areas inhabited by Spotted Owls is similar to forests where ecological restoration has occurred. Ecological restoration experiments have been conducted on relatively flat areas (<15% slope) and on southwestern-facing slopes (Covington and Moore 1994, Covington et al. 1997). In contrast, most Spotted Owl nests and roosts on our study area were located on the lower half of north-facing, moderate ($\bar{x}$ = 27.5%) slopes (RJG unpubl. data). Both slope aspect and percent slope affect fire behavior (Brown and Davis 1973, Whelan 1995); fire exclusion was one primary cause for the postsettlement changes in forest structure (Covington and Moore 1994, Covington et al. 1997). In addition, some historical evidence suggests topographically protected areas such as those inhabited by Spotted Owls may have had the dense structure of older forest (Cooper 1960, Shinneman and Baker 1997).

The importance of mature Gambel oak trees as key nesting sites for owls was evident in our study. Forty percent (34/84) of all nests found during this study were in oak cavities. At least two of these nest trees were felled by firewood cutters during our study even though live oak trees were protected. Oaks are important resources because they may allow not only occupancy of otherwise marginal habitat but also provide food and nest site resources for owl prey. In addition, they are critical resources to game birds (e.g., Wild Turkey, *Meleagris gallopavo*) and avifauna in general (Rosenstock 1998).

Current guidelines for the management of national forests within the range of the Mexican Spotted Owl encompass our recommendations regarding the retention of, and management for, mixed conifer habitat, residual trees, and large oaks (U.S. Dept. of Interior 1995, USDA Forest Service 1996). The primary contribution of this research to existing management plans relates to oaks. First, given the inability of current remote sensing equipment and classification procedures to detect understory oaks, locating this habitat component could be difficult. Therefore, we suggest on site ground verification in stands with dense canopies to estimate oak presence before proposed management activities occur. Second, though standing oaks are protected from harvest, no effective means exists to pre-

vent the poaching of live oaks. Therefore, we continue to recommend protection of all oaks, living or dead, throughout the pine-oak forest within the Mexican Spotted Owl's range (see also Seamans et al. 1999). Piñon-juniper woodlands offer a vast alternative fuel wood resource on our study area, creating no human hardship resulting from oak protection.

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APPENDIX. Definitions of vegetation types and descriptive statistics for map classification of the Mexican Spotted Owl study area, central Arizona, 1994.

Vegetation type	Basal area (m^2/ha) of live trees ≥45.7 cm dbh[a]		Canopy closure (%)	Study area coverage		Classification accuracy (%)	
	All species	Gambel oak		ha	%	Map[b]	Vegetation type[c]
Mature mixed conifer forest	≥6.89		≥55	1,579	2.7	67	80
Young mixed conifer forest	<6.89		≥55	1,228	2.1	91	91
Mature closed canopy forests of ponderosa pine and ponderosa pine-Gambel oak	≥6.89		≥55	7,894	13.5	78	64
Mature open canopy ponderosa pine forest	≥6.89		10–54	8,128	13.9	50	50
Mature open canopy ponderosa pine-Gambel oak forest	≥6.89	≥2.29	10–54	6,842	11.7	67	86
Young forests of ponderosa pine and ponderosa pine-Gambel oak	<6.89	<2.29	<10	22,923	39.2	86	82
Piñon pine-juniper woodland			<10	643	1.1	100	100
Nonforested			<10	9,239	15.8	83	100
Totals				58,476	100.0		

[a] Where values are absent, none were specified.

[b] The number of random locations (n = 88) of a given vegetation type that were classified correctly divided by the total number of random locations that were classified as that vegetation type, multiplied by 100.

[c] The number of random locations (n = 88) of a given vegetation type that were classified correctly divided by the total number of random locations assigned to that vegetation type based on field observation, multiplied by 100.

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HABITAT USE AND PRODUCTIVITY OF SHARP-SHINNED HAWKS NESTING IN AN URBAN AREA

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ABSTRACT.—We measured productivity and vegetation parameters of habitat quality at 16 Sharp-shinned Hawk (*Accipiter striatus*) nests in and near the greater Montreal area in order to evaluate nesting habitat use and its possible relationship to reproductive success in an urban setting. Mean clutch size was 4.4 and hatching success was 3.8 eggs per nest. At least one egg hatched in 11 of 16 nests (68.8%), 10 (62.5%) pairs raised young to a bandable age (≥10 days old), and 8 (50%) pairs successfully produced at least one fledgling. Immature individuals comprised 33.3% of male and 38.5% of female breeders. Mean values in the habitat assessment included nest tree height, 14.0 m; tree density, 955/ha; total canopy cover, 88.1%; coniferous cover, 39.7%; mean dbh, 17.6 cm; and distance to the nearest forest opening, 19.7 m. Sharp-shinned Hawks nested in a range of forest types, from mature conifer plantations to young, almost purely deciduous stands, and this population exhibited considerable flexibility with respect to most of the habitat features that we measured. Their use of older stands with more deciduous cover than those used by conspecifics elsewhere may reflect regional differences in habitat availability as well as in the abundance of competitor species. Breeding in an urbanized area does not seem to be detrimental to Sharp-shinned Hawks, as evidenced by this population's relatively large proportion of immature breeders and normal productivity, which appeared to be independent of all the assessed parameters of habitat quality. *Received 13 March 2002, accepted 30 August 2002.*

Knowledge of the habitat requirements of Sharp-shinned Hawks (*Accipiter striatus*) is important for understanding their nesting ecology and developing recommendations for their conservation and management. As habitat fragmentation is the principal threat to the survival of most temperate zone species (Wilcove et al. 1986), efforts to understand how urban populations respond to the lack of large tracts of wilderness become especially pertinent.

Vegetation and structural characteristics are important cues for birds seeking nest sites (Reynolds et al. 1982). For accipiters, these features often reflect successional stage (Reynolds et al. 1982, Newton 1991). Younger tree stands appear to provide the appropriate environmental conditions for breeding Sharp-shinned Hawks: dense stands of small-diameter trees, with relatively thick canopies and a high proportion of coniferous cover (Reynolds et al. 1982, Moore and Henny 1983, Wiggers and Kritz 1991, Trexel et al. 1999, Bildstein and Meyer 2000).

These characteristics may influence the ability of Sharp-shinned Hawks to nest successfully. For instance, their typical nest structure would not appear to favor the use of primarily deciduous stands since they build broad, flat nests, usually on horizontal branches, close to or touching the trunk (Bildstein and Meyer 2000). Building materials consist almost entirely of coniferous twigs and branches, probably because their nodules grip each other and help hold the nest together (Newton 1991). Also, as the smallest North American accipiters, Sharp-shinned Hawks are vulnerable to predation by many larger raptors; thus, nesting in stands that offer some concealment and in which bigger birds may have difficulty maneuvering provides protection (Bildstein and Meyer 2000).

Altering vegetation cover may have major impacts upon animal populations (Morrison et al. 1998). Previous studies (e.g., Viverette et al. 1996) suggested that declines in counts of eastern migrating Sharp-shinned Hawks during the 1980s and early 1990s may reflect decreased productivity in eastern populations, and that this might be related to losses of suitable breeding habitat. The coincidental increase in migrant Cooper's Hawks (*A. cooperii*) counted at eastern watch sites may indicate that forest aging and urbanization are

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benefiting this larger accipiter, whose productivity may be unaffected by urbanization (Rosenfield et al. 1996), while reducing breeding opportunities for Sharp-shinned Hawks (Viverette et al. 1996).

Few studies of Sharp-shinned Hawk nesting habitat have been conducted previously in eastern North America and none of these examined habitat use by Sharp-shinned Hawks breeding in human-dominated landscapes, or attempted to find evidence that such habitat changes are reflected in a decrease in this species' reproductive performance. Newton (1991) observed that the closely related European Sparrowhawk (*A. nisus*) in English and Scottish cities nested in "sub-standard" sites. He concluded that those birds used nesting habitat according to what was available to them. Accordingly, urban Sharp-shinned Hawks also might be expected to differ from non-urban birds in their use of nesting habitat. Any costs related to urbanization might result in reduced reproductive success. We studied habitat use and productivity to investigate this issue for Sharp-shinned Hawks nesting in the Montreal area. Our goal was to compare vegetation features of their nest sites and reproductive parameters with those of non-urban populations described in the literature.

METHODS

Study area.—Our approximately square 15,625-km^2 study area was centered at 45.52 N, 73.57 W in southwestern Quebec, in the St. Lawrence lowlands, which is characterized mainly by deciduous trees. The dominant geographical feature of the study area is the city of Montreal (population of 3.5 million in 1999), which, with its suburbs, covers a total area of 4,024 km^2 (Linteau 2000) or 26% of the study area.

The area was mostly forested prior to settlement, although more than 75% of it since has been cleared. The remaining woodlots, tree rows, and remnant stands do not support much of the wildlife that once lived there. In terms of green space, Montreal has 4,000 land parcels; 91% of these are <10 ha and 46% are <1 ha, with only 10% of the green space being wooded (Government of Canada 1996).

Nest searches.—We obtained historical nest card records from the Canadian Museum of Nature in Ottawa, and current reports of incidental sightings of Sharp-shinned Hawks from birdwatchers and wildlife technicians working in municipal and provincial parks. If we were able to determine that observers had made their observations in the course of random bird watching and not systematic nest searches, we used their information to locate potential nest sites.

Starting in late April at these locations, we searched a minimum 200-m radius area in all forest types on foot, using imitations of the territorial call of the Barred Owl (*Strix varia*) to elicit defensive responses from Sharp-shinned Hawks, if present. We also used visual evidence of nesting activity, such as whitewash, pluckings, or molted Sharp-shinned Hawk feathers to locate nests.

Data collection.—At each nest we identified the putative parents as immature (second year) or mature (after second year) based upon plumage. We counted eggs during late May, past the time when Sharp-shinned Hawks nesting at this latitude normally have begun to incubate (Bildstein and Meyer 2000, EAJ and L. Semo unpubl. data). To minimize disturbance, we used a pole-mounted mirror whenever possible.

At this latitude, Sharp-shinned Hawk eggs generally hatch in mid-June (EAJ unpubl. data), so we started checking nests for hatched eggs in early June, returning every few days until hatching was completed. We expressed hatching success as the percentage of hatched eggs per clutch. We could not assess clutch size and hatching success at six nests because of inaccessibility or because the nest had failed before we confirmed clutch size. Chicks ≥10 days old were considered bandable; three inaccessible nests were excluded from our calculation of bandable young per active nest (a nest in which eggs were laid, $n = 13$, or at which we observed a female in incubating posture, $n = 3$). Sharp-shinned Hawks leave the nest at 21–32 days of age and for the next few days tend to remain in the nest tree and other nearby trees (Bildstein and Meyer 2000), at which time they are counted easily. We had expected the chicks to fledge at about 27 days (EAJ unpubl. data), but many fledged earlier, making accurate fledgling counts impossible. We therefore report nesting success as the percentage of active nests that produced at least one fledgling.

After the young had fledged, we collected habitat data within 0.04-ha circular plots centered on each nest tree, following the technique of James and Shugart (1970) as modified by Titus and Mosher (1981). We ensured that all sites were independent according to the criteria of Rosenfield and Bielefeldt (1992, 1996). We identified the nest tree species and four most numerous canopy species using Rouleau (1990). We measured habitat variables (see Table 1) as in Trexel et al. (1999). Whenever possible, we determined stand age by consulting the landowner.

We compared several studies of Sharp-shinned Hawk nesting habitat with respect to the dispersion (standard deviations or standard errors) associated with selected habitat variables, expecting our urban population to exhibit relatively flexible habitat use. The most appropriate measure of dispersion for comparing variables from different populations with different sample sizes and means is the coefficient of variation (CV), which we calculated from SE and SD values (Freund and Wilson 1997).

TABLE 1. Habitat characteristics for 16 Sharp-shinned Hawk nests in the Montreal area of Quebec, Canada, 1999–2001, demonstrating high variability for most habitat features, low variability for some.

Variable	Mean ± SE	Coefficient of variation (%)
Nest height (m)	9.5 ± 1.0	41.8
Nest tree height (m)	14.0 ± 1.3	38.5
Nest tree condition (%)	48.0 ± 9.0	74.0
Nest tree dbh (cm)	24.7 ± 2.6	42.1
Canopy height (m)	15.1 ± 1.4	37.3
Total canopy cover (%)	88.1 ± 2.2	10.1
Deciduous cover (%)	48.4 ± 7.0	57.8
Coniferous cover (%)	39.7 ± 6.2	62.0
Understory cover (%)	34.5 ± 7.4	86.1
Ground cover (%)	29.1 ± 4.7	64.1
Shrub density[a] (no. of tall shrubs/plot)	29.0 ± 9.0	100.0
Shrub index[a] (no. of low shrubs/plot)	55.0 ± 13.0	79.0
Tree density (trees/ha)	955.0 ± 155.0	65.0
Understory density[a] (trees/ha)	44.0 ± 18.0	135.0
Basal area of trees (m^2/ha)	28.7 ± 3.5	49.0
Mean dbh (cm)	17.6 ± 1.8	41.9
Distance to water[b] (m)	60.0 ± 22.3	111.7
Distance to opening (m)	19.7 ± 5.1	102.8
Stand age (years)[c]	44.0 ± 7.0	43.0

[a] Variable not assessed at five nests.
[b] Variable not assessed at seven nests where location of nearest water source was unknown.
[c] Variable not assessed at eight nests where age of stand was unknown.

RESULTS

Nesting.—Of the putative breeders for which age was determined, 38.5% of females and 33.3% of males were immature. Both putative parents were immature at 3 of 16 nests. Mean clutch size was 4.4 (range, 4–5; n = 10). The mean number of eggs hatched per active nest (n = 10) was 3.8 (range, 0–5) and mean hatching success was 77.7%. Ten of 16 pairs (62.5%) raised ≥1 chick to bandable age, but we counted bandable nestlings at only seven nests, where the mean number of bandable young was 3.9 (range, 2–5). The mean number of bandable young per active nest (n = 13) was 2.1 (range, 0–5), with 8 of the 16 nests successfully fledging ≥1 young.

Habitat.—All nests (n = 16) were in conifers, including four in white spruce (*Picea glauca*); two each in Norway spruce (*P. abies*), black spruce (*P. mariana*), jack pine (*Pinus banksiana*), white cedar (*Thuja occidentalis*), and eastern hemlock (*Tsuga canadensis*); and one each in white pine (*Pinus strobus*) and balsam fir (*Abies balsamea*). At all but two sites, conifers were well represented in the canopy. Thirteen stands were mixed, and none were monospecific. The species most commonly present in the surrounding canopy were red and sugar maple (*Acer rubrum* and *A. saccharum*); grey, paper, and yellow birch (*Betula populifolia*, *B. papyrifera*, and *B. alleghaniensis*); trembling poplar (*Populus tremuloides*), American beech (*Fagus grandifolia*), white ash (*Fraxinus americana*), red oak (*Quercus rubra*), and red pine (*P. resinosa*).

Mean stand age was 44 years (range, approximately 30–100 years). Means and coefficients of variation for the other habitat variables are given in Table 1.

Nesting success was not significantly correlated with either tree density (r = 0.18, n = 16, P = 0.51) or distance to nearest opening (r = 0.14, n = 16, P = 0.59).

DISCUSSION

The Sharp-shinned Hawks in and near Montreal nested closer to openings ($\bar{x}$ = 19.7 m) than conspecifics in Wisconsin ($\bar{x}$ = 58 m; Trexel et al. 1999) or Arkansas ($\bar{x}$ = 46 m; Garner 1999). In many cases, the nearest openings were areas of considerable human activity, including cycling or walking trails and a golf course. One nest, which was successful, was along a heavily used all-terrain vehicle trail and another, which failed, was a few meters from the main road in Montreal's Botanical Gardens. This close proximity to edges may reflect a relative scarcity of large tracts of forest in this study area.

Every Sharp-shinned Hawk nest we found was in a conifer, regardless of the type of stand. Trexel et al. (1999) reported a similarly disproportionate tendency for Sharp-shinned Hawks to use conifers in mixed forest. However, our population used stands with the least coniferous cover ($\bar{x}$ = 39.7%) and most deciduous cover ($\bar{x}$ = 48.4%) of all studies we examined (cf. 61.3% and 15.2%, respectively, in Trexel et al. 1999). This result may reflect regional differences in vegetation across North America. Our study area was in the deciduous forest vegetation zone (Rouleau 1990). Additional studies of habitat use by nesting Sharp-shinned Hawks elsewhere in

this zone may elucidate whether this pattern is common among northeastern populations.

The mean age of stands used by this population was 44 years, similar to the finding in Oregon (25–50 years; Reynolds et al. 1982). However, stand structure presumably is more important than age with respect to its suitability for nesting Sharp-shinned Hawks. While the Douglas fir (*Pseudotsuga menziesii*), western hemlock (*T. heterophylla*) and ponderosa pine (*P. ponderosa*) of Oregon's forests are still young at 50 years old, many northeastern conifers are approaching maturity at this age (Burns and Honkala 1990).

That Sharp-shinned Hawks nested in structurally mature stands may be related to the status of the Cooper's Hawk (a predator and competitor of the Sharp-shinned Hawk) in the area. There are an estimated 60 breeding pairs of Cooper's Hawks in Quebec (Barnhurst et al. 1996, Bird 1999) and only 15 nest sites were found in our study area during the past 10 years. Many of the structurally older stands they ordinarily would inhabit are unlikely to contain breeding pairs (Barnhurst et al. 1996), leaving more areas for Sharp-shinned Hawks to nest.

Low Cooper's Hawk numbers similarly may explain the comparatively high deciduous cover for the nest sites of our Sharp-shinned Hawk population. The study by Trexel et al. (1999) is an interesting contrast: since Wisconsin delisted the Cooper's Hawk in 1989 (Rosenfield and Bielefeldt 1993), it may have become the most numerous forest hawk in that state (Bielefeldt et al. 1998). There, stands used by nesting Sharp-shinned Hawks were denser, with more coniferous cover than those used by Cooper's Hawks in the same region, or by Sharp-shinned Hawks in our study. If the Cooper's Hawk population also is increasing in Quebec (F. Shaffer and P. Fradette pers. comm.), revisiting this issue in the future might reveal different patterns of habitat use by nesting Sharp-shinned Hawks.

The fact that this population of Sharp-shinned Hawks nested in more open sites, with more large, deciduous trees than other populations, may suggest a link between urbanization and nesting habitat use. Yet, it is difficult to separate differences in forest type due to urbanization from those due to geography. It also is impossible to compare current patterns of habitat use by nesting Sharp-shinned Hawks in such an established urban environment with patterns they exhibited prior to development. Comparing the nest sites used by urban and rural populations in a single geographic area might provide a more accurate assessment of differential patterns of nesting habitat use as they relate specifically to urbanization.

Measures of dispersion may be important in assessing a population's flexibility with respect to nesting habitat and the ability to adapt to habitat change. Contrary to our expectation that this urban population would exhibit more plasticity than rural ones, our results suggest that this species may not have stringent requirements for the majority of habitat variables we measured. Despite their ability to nest in different forest types, Sharp-shinned Hawks generally may be restricted to well-covered stands. Whereas variation in most other variables was high, CV values for canopy cover ranged from 7.7% in Wisconsin (Trexel et al. 1999) to 35.5% in eastern Oregon (Reynolds et al. 1982), with a mean of 17.1% for all studies examined.

Mean clutch size in our study (4.4) was within the range (3–8 eggs, usually 4 or 5) reported for Sharp-shinned Hawks breeding in temperate climates (Bildstein and Meyer 2000). Mean clutch sizes were 4.3 in Utah (Platt 1976), 4.4 in Wisconsin (L. Semo et al. unpubl. data), 4.5 in Missouri (Wiggers and Kritz 1994), 4.6 in Oregon (Reynolds and Wight 1978), and 3.9 in North America overall (Apfelbaum and Seelbach 1983).

Mean hatching success (77.7%) and mean brood size (3.8) were within the range of previously reported values. Hatching success rates for Sharp-shinned Hawks were 70% in Oregon (Reynolds and Wight 1978) and 87% in New Brunswick (Meyer 1987). In Missouri, Wiggers and Kritz (1994) reported a mean brood size (number of young in nest on first visit after hatching) of 3.5 chicks. The North American mean was 2.7 nestlings per nest (Apfelbaum and Seelbach 1983), but it is unclear whether this figure refers to hatching success or brood size (Bildstein and Meyer 2000). Our mean number of nestlings that reached a bandable age (3.9) was similar to that found by EAJ (3.6; unpubl. data) during 13 years in Wisconsin.

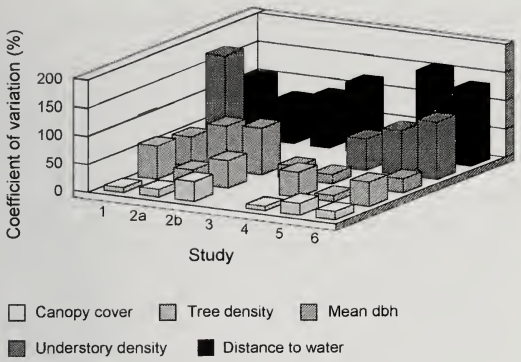

FIG. 1. Variation in habitat characteristics of 16 Sharp-shinned Hawk nest sites in the Montreal area from 1999–2001, and at nests of other populations, demonstrating flexibility with respect to most habitat variables (high CV values) and relative stringency with respect to canopy cover (low CV values). The studies were conducted in (1) Quebec, the present study; (2a) northwestern Oregon, Reynolds et al. 1982; (2b) eastern Oregon; Reynolds et al. 1982; (3) northeastern Oregon, Moore and Henny 1983; (4) Missouri, Wiggers and Kritz 1991; (5) Arkansas, Garner 1999; and (6) Wisconsin, Trexel et al. 1999.

In contrast, our nesting success (50%) was low compared to those found in Oregon (91.7%; Reynolds and Wight 1978), New Brunswick (95%; Meyer 1987), and Wisconsin (76%; L. Semo et al. unpubl. data). The mean number of young banded per nest attempt (2.1) in our study also was low compared to 2.7 in Wisconsin (L. Semo et al. unpubl. data). Weather conditions may have contributed to our high rate of nest failures. Inclement weather can reduce prey availability and hunting efficiency for raptors while increasing their energy requirements, resulting in elevated nestling mortality. Wet weather has been linked to reduced productivity in Ospreys (*Pandion haliaetus*; Odsjö and Sondell 1976), Black Eagles (*Aquila verreauxii*; Gargett 1977), and European Sparrowhawks (Newton 1991). In our study, all but one nest failure occurred during the summer of 2000, which arrived late and was unseasonably cold and rainy (A. Julien pers. comm.).

Other birds of prey, such as the Red-shouldered Hawk (*Buteo lineatus*), Eastern Screech-Owl (*Otus asio*), and Mississippi Kite (*Ictinia mississippiensis*), seem to be equally or more productive in urban areas than in rural areas (Dykstra et al. 2000, Gehlbach 1996, Parker 1996, respectively). Rosenfield et al. (1996) found that Cooper's Hawks breeding in an urban and suburban area of Wisconsin not only had relatively large clutch sizes and numbers of bandable young, but also nested at the highest nesting density ever recorded for this species.

We detected no relationships between productivity and parameters of habitat quality. For example, if forest fragmentation were impairing Sharp-shinned Hawk productivity, we would have expected pairs that nested closer to edges to perform comparatively poorly. Similarly, if forest aging were reducing the productivity of Sharp-shinned Hawks which, according to many studies (Reynolds et al. 1982; Moore and Henny 1983; Wiggers and Kritz 1991; Trexel et al. 1999; Bildstein and Meyer 2000), nest mainly in dense woods, breeders would tend to be less successful in more open stands. Larger sample sizes are required to adequately address these questions.

Our percentage of immature breeders (36%) was high, we found similar numbers of males and females among yearling breeders, and pairings between yearlings occurred at least 18.8% of the time. During 10 years in Scotland, 18% of fathers and 15% of mothers at European Sparrowhawk nests were immature, and few adult-immature pairs were observed. Productivity was lower for adult-yearling pairs than adult pairs, and lowest for yearling pairs (Newton 1991). In contrast, adult male-yearling female Sharp-shinned Hawk pairs in Wisconsin were no less productive than pairings between adults, and both performed better than pairs containing immature males. Immature females in Wisconsin also bred >2.5× more often than immature males (EAJ and L. Semo unpubl. data), while juvenile male sparrowhawks in Scotland bred only 1.2× more often than juvenile females (Newton 1991). Furthermore, only 4.6% and 6.3% of pairs in Wisconsin and Scotland, respectively, were between yearlings, and in Scotland, the highest percentage of yearling-yearling pairs reported in any one year was 13.5%.

A longer term study could examine whether our Sharp-shinned Hawk population consistently contains more immature breeders than other populations, and if so, what this reveals about environmental conditions and demographics in our area. Higher proportions of

yearling breeders may be observed when environmental conditions are especially favorable for breeding (Newton 1979), or, alternately, when habitat is less than ideal and more suitable habitat elsewhere is occupied by more experienced, adult breeders (D. R. Trexel pers. comm.).

Cities tend to support a lower diversity of raptors, as do smaller parcels of woodland. However, this population bred successfully in these fragments, which were wooded and had well-covered canopies. As Montreal continues to develop outward, small fragments of forest are lost; their importance to local and regional wildlife populations may be unrecognized. We believe that remaining stands of forest should be considered as potential nest sites for Sharp-shinned Hawks and other raptors, and every possible effort should be made to protect them from being cleared.

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SEASONAL VARIATION IN SEX RATIO OF FLEDGLING AMERICAN KESTRELS: A LONG TERM STUDY

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ABSTRACT.—The Early Bird Hypothesis predicts that males fledged early in the breeding season have an advantage over their later-fledged counterparts during competition for breeding sites. We tested this hypothesis by examining the sex ratio of 1,025 fledglings from 265 broods of American Kestrels (*Falco sparverius*) breeding in nest boxes in Wisconsin during the period 1968–1997. We found a seasonal shift in the sex ratio: the sex ratio of fledglings was biased toward males early in the breeding season, but became increasingly biased toward females as the season progressed. Our results provide support for the Early Bird Hypothesis and suggest that the steepness of this trend may decrease with increasing latitude. *Received 10 December 2001, accepted 5 July 2002.*

The offspring sex ratio in most species of birds rarely differs from parity (Clutton-Brock 1986, Koenig and Dickinson 1996). Nonetheless, recent studies have documented many exceptions from parity (Gowaty 1993, Ellegren et al. 1996, Svensson and Nilsson 1996, Komdeur 1996). In particular, several species of raptors showed a seasonal shift in the sex ratio, although the total annual number of male and female offspring was equal. In the Eurasian Kestrel (*Falco tinnunculus*; Dijkstra et al. 1990, Daan et al. 1996) and Lesser Kestrel (*Falco naumanni*; Tella et al. 1996) the fledgling sex ratio was skewed toward males early in the season while late broods had an excess of females. Recently the same seasonal trend was found in a Florida population of the American Kestrel (*Falco sparverius*; Smallwood and Smallwood 1998), but not in a Canadian population of the same species (Wiebe and Bortolotti 1992, and see Smallwood and Smallwood 1998). Differential parental investment (Trivers and Willard 1973), local competition for resources between parent and offspring (Gowaty 1993, Komdeur 1996), species life history traits (Daan et al. 1996), and intrasexual competition for the nest site (Smallwood and Smallwood 1998) are among the most common hypotheses to explain the adaptiveness of biased sex ratios. In raptors, breeding parameters such as brood size, breeding success, and laying date may change according to food availability, population density, or weather conditions, showing great interannual and seasonal variation (Newton 1979, Kostrzewa and Kostrzewa 1990).

Although within season variation in sex ratio has been documented, interannual variation rarely has been considered in previous studies because long term data usually are lacking (Olsen and Cockburn 1991, Gowaty 1993, Weatherhead and Montgomerie 1995, Leroux and Bretagnolle 1996). We studied sex ratio variation of fledglings (tertiary sex ratio, *sensu* Smallwood and Smallwood 1998) in a population of American Kestrels from 1968 to 1997 in order to investigate interannual and intraseasonal variation in fledgling sex ratio. Furthermore, we compared the results from the Canadian and Florida populations to those from our Wisconsin population, which occurs at an intermediate latitude.

METHODS

We conducted the study in central Wisconsin (44° 13′ N, 89° 30′ W) in a 20,243-ha area. This area consists almost entirely of prairie and marshes with cultivated fields and woodlots. Each year from 1968 to 1997 we visited a mean of 50 (range 45–54) nest boxes provided specifically for kestrels about five times during the breeding season (range: 3–7; see Hamerstrom et al. 1973 for details). Young were sexed about one week before fledging on the basis of plumage (alar tract feathers; Smallwood and Smallwood 1998). We analyzed data on offspring sex ratio using only those

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TABLE 1. Models of the proportion of female fledglings in American Kestrel (*Falco sparverius*) broods as a function of year and of the laying date. Analyses are based on 265 broods (1,025 fledglings) in central Wisconsin, 1968–1997. The names 'laying date' or 'Laying Date' are models where the eight 15-day classes were considered as a factor or a continuous variable, respectively, and their interaction is noted 'x.' In model notation '+' indicates the absence of interaction and '·' when no effects were present, np = number of estimable parameters in the model, and AIC = deviance + 2 × np.

Model and notation	np	Deviance	AIC	AIC Diff	Rel Diff	AIC weights
1 Laying Date	2	305.7	309.7	0.0	188.4	0.877556
2 laying date	8	298.1	314.1	4.4	270.3	0.097236
3 ·	1	314.8	316.8	7.1	298.1	0.025207
4 Laying Date + year	29	280.0	338.0	28.3	289.4	6.28E-07
5 laying date + year	35	270.3	340.3	30.6	314.8	1.99E-07
6 year	28	289.4	345.4	35.7	305.7	1.55E-08
7 laying date × year	96	188.4	380.4	70.7	280.0	3.9E-16

nests for which all offspring were sexed and the clutch initiation date was known (for this reason the years 1986 and 1987 were excluded). We determined the clutch initiation date from the number of eggs in an incomplete clutch (this occurs in a large part of our dataset) or alternatively by backdating from the observed or inferred hatching date. The amount of error is negligible with respect to the 15-day date categories that we used. The proportion of female fledglings was modeled as a binomial variable using year and laying date as independent variables. Interannual variation was first investigated considering year as a random term in linear mixed models (procedure GLMM in GENSTAT 5.0 ver. 3.1; GENSTAT 5 Committee 1993), but the variance component was negative. We thus considered year as a fixed factor in generalized linear models in order to test an additive relationship between the two effects. Model selection followed the Akaike Information Criterion value (AIC; Burnham and Anderson 1998). This is the sum of the model deviance and twice the number of parameters in the model. We considered the model with the lowest AIC value to be the best compromise between description of the data (model deviance) and parameter used in the model. Finally, there were insufficient data to include brood size as a dependent variable in the model. Its influence on the pattern of offspring sex ratio was analyzed using chi-square analysis on pooled data (no year effect) as in Rosenfield et al. (1996). In this analysis we also included the broods for which clutch initiation dates were not known precisely (see above). For all analyses the significance level was set at $P \leq 0.05$.

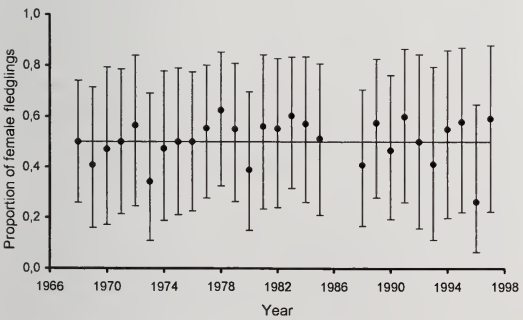

FIG. 1. Change in the proportion of female fledglings estimated from model 4 in Table 1. Analyses are based on 265 broods (1,025 fledglings) of American Kestrels (*Falco sparverius*) in central Wisconsin, 1968–1997. Bars indicate 95% confidence intervals. The horizontal line indicates the value of 0.5. Data from year 1986 and 1987 were excluded because laying date was not known precisely (see Methods).

RESULTS AND DISCUSSION

We modeled fledgling sex ratio in a total of 265 broods (1,025 fledglings) collected over 28 years (1968–1997) for which the first laying day was known. Afterwards, we determined that the extrabinomial variance was not significant ($X^2_{169} = 188.4$, $P = 0.15$), indicating that the effects of year, laying date, and their interaction provided a good description of the data in our model. We obtained a first important reduction in AIC value by dropping the interaction term (Table 1). A further reduction occurred when we did not consider the year effect (model 3 in Table 1). In contrast, the AIC value increased when the effect of laying date was dropped (model 4 in Table 1; Fig. 1). Indeed, the proportion of females on cumulated data was not significantly different from 0.5 (0.51, range: 0.48–0.54, from model 5) but seemed to increase with laying date. Modeling offspring sex ratio as a continuous linear function of the laying date provided a more parsimonious description of the data as indicated by the low AIC value of model 6 (Table 1). The regression model was

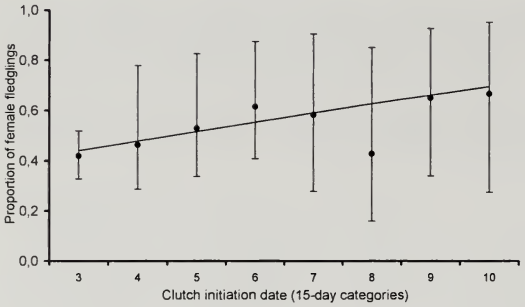

FIG. 2. Seasonal changes in the sex ratio in the American Kestrel (*Falco sparverius*) breeding in central Wisconsin, 1968–1997 (1,025 fledglings). The line indicates the values expected when the proportion of female fledglings is modeled as a continuous function of the laying date classes. Bars indicate 95% confidence intervals.

logit $(f) = -0.69 + 0.15x \times L_{i,}$ where f is the proportion of female fledglings and L_i is the 15-day class i from 31 March (Fig. 2). Even in this more parsimonious environment (i.e., few effects are considered), the model assuming an additional effect of the year still was not retained (model 7 in Table 1). Finally, we detected no significant effect of brood size on fledgling sex ratio ($X^2_5 = 3.58$, $P = 0.61$; Table 2).

Sex biased mortality of nestlings may occur at different stages of the nesting period. The primary sex ratio is the sex ratio at fertilization, whereas a biased secondary sex ratio may occur through differential mortality of eggs. For example, Anderson et al. (1993) suggested that the observed sex-biased mortality of American Kestrel nestlings was due to the female chicks' competitive dominance over their male siblings. However, the sex of individual unhatched eggs was unknown and the sex of the young that did not fledge was not reported. Therefore, the mechanism by which these broods were biased is unknown. Nevertheless, we may consider alternative hypotheses for a male's fitness advantage of fledging early in the breeding season.

The Local Resource Competition Hypothesis (LRC) predicts that parents should produce a sex ratio biased in favor of the less competitive sex (Gowaty 1993, 1997). Therefore, LRC predicts that parents should bias their broods in favor of the sex that disperses farthest, but it cannot explain why sex ratio changes significantly during the breeding season.

TABLE 2. Sex ratio by brood size of American Kestrels (*Falco sparverius*) in central Wisconsin, 1968–1997 (1,197 fledglings).

Brood size	Number of broods	Number of females	Number of males	% females
1	13	6	7	46.2
2	30	30	30	50.0
3	51	82	71	53.6
4	101	201	203	49.8
5	111	285	270	51.4
6	2	9	3	75.0
Total	308	613	584	51.2

An alternative hypothesis, proposed by Daan et al. (1996), to explain a seasonal shift in offspring sex ratio was based on size and sex specific differences in maturation time (age at first breeding). This Maturation Time Hypothesis (MTH) was modified from a general theory first proposed by Trivers and Willard (1973). For raptor species in which first breeding occurs early in life (e.g., the Eurasian Kestrel), the MTH predicts that early broods should be male biased because while all females start breeding at one year of age, only males from early clutches start at one year of age (Dijkstra et al. 1990). In contrast, raptor species with delayed maturation should have female biased broods. Thus, although the MTH explains differences in the pattern of the seasonal variation in sex ratio of some raptor species (Daan et al. 1996), it does not support the pattern shown by the American Kestrel in which males usually breed at one year of age (Del Hoyo et al. 1994). We do not know if age at first breeding varies latitudinally in American Kestrels. If so, then our findings might simply provide further support for the MTH.

However, the MTH does not consider the ecological conditions that confer sex specific advantages, such as availability of suitable nest sites (see Smallwood and Smallwood 1998). Smallwood and Smallwood (1998) proposed the Early Bird Hypothesis (EBH), suggesting that for nonmigratory populations that are nest site limited, early-fledged males are at a competitive advantage over later-fledged males since breeding territories are acquired during post-fledging dispersal (see also

Balgooyen 1976); no such advantage would occur in migratory populations, since territory acquisition occurs at the end of spring migration. Thus, the EBH accounts for the differences between the nonmigratory population studied in Florida and the migratory one studied in Canada, in which seasonal shift in sex ratio was not observed (Wiebe and Bortolotti 1992).

In the present study, we found evidence of a seasonal shift in sex ratio, despite the fact that our population is migratory. Because our study population in central Wisconsin is at an intermediate latitude relative to the Florida and Canada populations, we suggest that the seasonal sex ratio bias decreases from south to north. Three factors are consistent with this suggestion. First, our population is in the geographical limit of the migratory and nonmigratory areas (Del Hoyo et al. 1994). Second, the proportion of males does not vary greatly in our population (range: 0.41–0.53) compared to that of the Florida population (range: 0.36–0.58; Smallwood and Smallwood 1998). Third, in our study area the natural breeding sites (natural holes in large trees) were not abundant (only nine natural nests detected during 50 years of study; see also Hamerstrom et al. 1973) contrary to that observed in the study sites used by Wiebe and Bortolotti (Bortolotti and Iko 1992). Thus, there was considerable competition for suitable breeding sites.

In conclusion, our long term study supports the predictions of the EBH. Moreover this study suggests a latitudinal gradient of this effect may exist, as recently predicted by Pen et al. (1999) in a statistical model generated from an evolutionarily stable strategy approach to the brood sex ratio question.

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TIMING AND MAGNITUDE OF BROAD-WINGED HAWK MIGRATION AT MONTCLAIR HAWK LOOKOUT, NEW JERSEY, AND HAWK MOUNTAIN SANCTUARY, PENNSYLVANIA

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ABSTRACT.—The Broad-winged Hawk (*Buteo platypterus*) breeds in eastern and central Canada and the United States, and winters in Central America and northern and central South America. Birders and ornithologists count migrating Broad-winged Hawks at dozens of traditional watch sites throughout the northeastern United States. We modeled counts of migrating Broad-winged Hawks from two raptor migration watch sites: Montclair Hawk Lookout, New Jersey, and Hawk Mountain Sanctuary, Pennsylvania, to determine whether annual abundance and trend estimates from individual sites within the mid-Atlantic states are representative of the region as a whole. We restricted ourselves to counts made between 10:00 and 16:00 EST during September to standardize count effort between sites. We created one model set for annual counts and another model set for daily counts. When modeling daily counts we incorporated weather and identity of individual observers. Akaike's Information Criteria were used to select the best model from an initial set of competing models. Annual counts declined at both sites during 1979–1998. Broad-winged Hawk migration began, peaked, and ended later at Montclair than at Hawk Mountain, even though Hawk Mountain is 155 km west-southwest of Montclair. Mean annual counts of hawks at Montclair were more than twice those at Hawk Mountain, but were not correlated. Broad-winged Hawks counted at Montclair may not be the same birds as those counted at Hawk Mountain. Rather, the two sites may be monitoring different regional subpopulations. Broad-winged Hawks counted at the two sites may use different migration tactics, with those counted at Hawk Mountain being more likely to slope soar, and those at Montclair more likely to use thermal soaring. A system of multiple watch sites is needed to monitor various breeding populations of this widely dispersed migrant. *Received 17 May 2002, accepted 24 August 2002.*

The Broad-winged Hawk (*Buteo platypterus*) is a small, forest-dwelling, migratory buteo that breeds in central and eastern Canada and the United States and overwinters in Central America and northern and central South America (Goodrich et al. 1996). Migrating Broad-winged Hawks typically travel in loosely organized, cluster flocks (*sensu* Heppner 1974) that can include thousands and even tens of thousands of birds (Bildstein 1999, Zalles and Bildstein 2000). Most of their long distance flight consists of slope soaring and thermal soaring interspersed with interthermal gliding (Kerlinger et al. 1985, Bildstein 1999). During autumn, scattered opportunities for slope soaring along mountain ridges, and a lack of thermals over large bodies of water, concentrate migrants in many locations. In the U.S., large concentrations occur along the northern shores of the Great Lakes, the eastern edges of the Appalachian Mountains, the coastal zone of southern New England, and the coastal plain of southern Texas. Farther south, large concentrations occur along coastal Veracruz, Mexico, in southeastern Costa Rica, and over the Pacific slope of Panama (Sutton and Sutton 1999, Bildstein and Saborio 2000, Zalles and Bildstein 2000).

During the late 1990s, more than 150 raptor migration watch sites were recording the annual southbound movements of this species (Zalles and Bildstein 2000). However, most analyses of Broad-winged Hawk migration have focused on annual variation in counts at single watch sites (Kerlinger et al. 1985, Bednarz et al. 1990, Allen et al. 1996, Bildstein 1998). Our understanding of the geography of Broad-winged Hawk migration remains rudimentary, particularly regarding the extent of broad-frontal leading-line movements, and identity of source populations of birds counted at particular watch sites (Kerlinger et al. 1985, Zalles and Bildstein 2000).

We were specifically interested in whether

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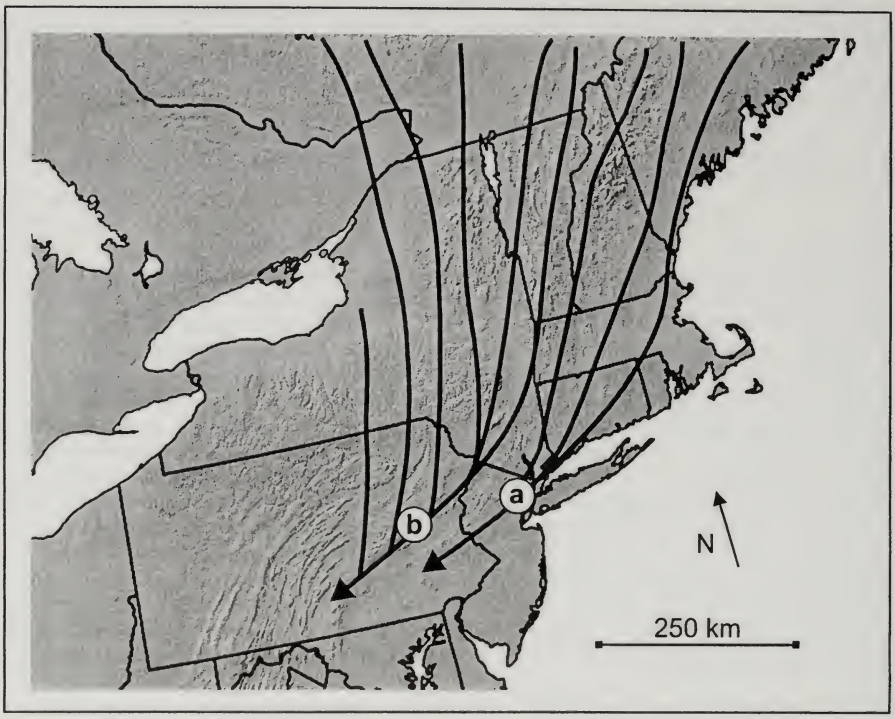

FIG. 1. Locations of Montclair Hawk Lookout (a) and Hawk Mountain Sanctuary (b), with hypothesized flight lines of migrating Broad-winged Hawks in the region.

annual counts of Broad-winged Hawks made from a single watch site were representative of the autumn migration in the northeastern U.S., and therefore suitable alone for monitoring that population. Thus, we compared the timing and magnitude of the autumn flight of Broad-winged Hawks at two ridgetop watch sites in eastern North America along approximately the same latitude but separated longitudinally by approximately 155 km. Hawk Mountain Sanctuary is an inland raptor migration watch site in the central Appalachian Mountains of eastern Pennsylvania (Bildstein 1998). Montclair Hawk Lookout is a coastal lowland watch site in northeastern New Jersey (Zalles and Bildstein 2000).

If Broad-winged Hawks migrate southwest along a broad front through northeastern North America, we predicted the magnitude and timing of migration at the two sites would correlate, with the timing of movements at Hawk Mountain lagging that of Montclair. If instead regional subpopulations of Broad-winged Hawks migrate independently of each other, then the magnitude of the flight at the two sites would vary independently, and the timing of the flight at Hawk Mountain need not lag that of Montclair.

METHODS

We analyzed autumn migration counts of Broad-winged Hawks from Montclair Hawk Lookout and Hawk Mountain Sanctuary. Montclair Hawk Lookout (155 m elevation) is in northeastern New Jersey (40° 50′ N, 74° 12′ W; Fig. 1), 30 km northwest of New York City, on First Watchung Mountain, the first ridge west of the lowermost Hudson River. Hawk Mountain Sanctuary is a 465-m ridgetop watch site along the Kittatinny Ridge in eastcentral Pennsylvania (40° 38′ N, 75° 59′ W), 170 km west of New York City (Broun 1949).

Migrating Broad-winged Hawks have been counted at Hawk Mountain since 1936 (excluding 1943–1945), and at Montclair Hawk Lookout since 1957 (Zalles and Bildstein 2000). Both sites conduct migration counts on most days from at least 1 September through mid-November. Annual counts at both sites regularly exceed 8,000 birds. We restricted our analysis to counts made during 1979–1998, in part because the number of count days at Montclair increased from 22 to 86 days during 1966–1974 but remained relatively constant thereafter (varying between 86 and 103 days). Also, the 1978 count at Hawk Mountain was anoma-

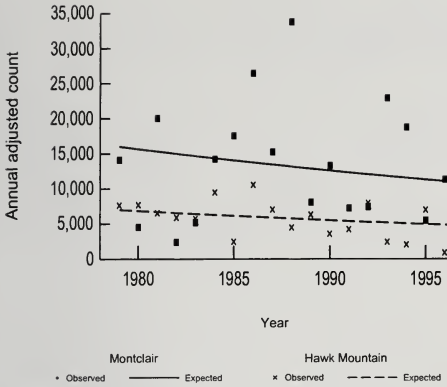

FIG. 2. Adjusted counts of Broad-winged Hawks observed and expected each September at Montclair Hawk Lookout, New Jersey, and Hawk Mountain Sanctuary, Pennsylvania, 1979–1998.

lously large (i.e., 98% larger than the next largest count of Broad-winged Hawks ever recorded at Hawk Mountain). We felt including this outlier could bias our results.

Annual counts from both sites were modeled together by including a site variable in the model. Counts often did not begin or end at the same time of day at both sites. We therefore standardized count effort between sites by restricting analyses to birds counted during September between 10:00 and 16:00 EST.

We also modeled daily counts adjusted for effort. A set of 11 competing models was created. Most of these models included site, year, and day of year. Some models of daily counts included primary observer, maximum visibility, wind direction, or change in temperature or cloud cover during the previous 24 h (Sauer et al. 1994, Allen et al. 1996), using weather data collected at noon. The observer assigned for a given day was the most experienced official counter present at noon.

We conducted model selection of annual and daily counts by first constructing a global model including all variables (Burnham and Anderson 1998). Parameters were estimated using SASRalph (ver. 16, November 2000, available from G. Pendleton, Alaska Dept. of Fish and Game, Douglas). SASRalph models count data using generalized linear models, a Poisson distribution, no intercept, and a variation of Proc GENMOD in SAS to adjust for overdispersion (Link and Sauer 1997, SAS Institute, Inc. 1997). We conducted model selection using Akaike's Information Criterion corrected for small sample size (AIC*c*, Burnham and Anderson 1998). The AIC finds an optimal balance between model fit (i.e., number of parameters) and precision (i.e., bias). The model with the lowest AIC*c* value was considered best.

Variables potentially unrelated to trend were removed from the global model one at a time. If the resulting constrained model had a lower AIC*c* value than the more general model, we permanently discarded the variable under consideration. Otherwise, we retained that variable. We estimated Akaike weights for each model and examined model-averaged parameter estimates if no model had an Akaike weight >0.95 (Anderson et al. 2001, Burnham and Anderson 1998).

We compared the timing of migration between sites by modeling mean daily counts during 1979–1998 using Proc GEMNOD with a normal distribution and an identity link. We also compared the mean daily cumulative percent of the annual flight at each watch site. Lastly, we tested for a correlation between annual adjusted total counts at the two sites using Proc GENMOD with a Poisson distribution. Standard errors of parameter estimates are reported unless stated otherwise.

RESULTS

During 1979–1998 mean annual Broad-wing Hawk counts at Montclair ($\bar{x}$ = 13,119, SD = 8,260) were more than twice those at Hawk Mountain ($\bar{x}$ = 5,716, SD = 2,653). The best model of annual counts included a site effect ($\beta_{\text{Montclair}} = 9.47 \pm 0.15$ versus $\beta_{\text{Hawk Mountain}} = 8.64 \pm 0.10$, $P < 0.001$ for both sites, $df_{\text{Montclair}} = 1$, $\chi^2_{\text{Montclair}} = 4{,}175$, $df_{\text{Hawk Mountain}} = 1$, $\chi^2_{\text{Hawk Mountain}} = 6{,}873$) and a negative year effect ($\beta_{\text{year}} = -0.02 \pm 0.02$, $P = 0.14$, df = 1, $\chi^2 = 2.21$; Fig. 2), but no site × year interaction, suggesting that counts at both sites declined during this period (Table 1). Model-averaged parameter estimates were virtually identical to those given above.

The best model of daily counts during

TABLE 1. Models of annual adjusted counts of Broad-winged Hawks at Montclair Hawk Lookout, New Jersey, and Hawk Mountain Sanctuary, Pennsylvania, during 1979–1998. A total of 40 observations were used in these models.

Model number	Model	Number of parameters	AIC_c	Delta AIC_c	Akaike weight
1	site + year	3	745.810	0.00	0.42
2	site	2	746.243	0.43	0.34
3	site + year + year × site	4	746.930	1.12	0.24

TABLE 2. Models of daily adjusted counts of Broad-winged Hawks at Montclair Hawk Lookout, New Jersey, and Hawk Mountain Sanctuary, Pennsylvania, during 1979–1998. A total of 948 observations were used in these models.

Model number	Model	Number of parameters	AIC_c	Delta AIC_c	Akaike weight
1*	site + julian × site + visibility	7	10812.5	0.00	0.59
2	julian × site + visibility	6	10814.8	2.28	0.26

* Expected values from this model were identical to those from a model with: site + julian + julian × site + visibility.

1979–1998 included site, day, site × day, and maximum visibility (Tables 2 and 3). No annual trend was detected. The flight tended to be smaller at Montclair than at Hawk Mountain during the first week of September, but larger at Montclair than at Hawk Mountain later in the month. Fewer birds were counted on very hazy days, when maximum visibility was <3.2 km.

The Akaike weight for the lowest AIC*c* model of daily counts was more than twice that of the next best model (0.59 versus 0.26; Table 2). The second-best model of daily counts differed from the best model only in not including a main site effect. No other model had an Akaike weight >0.07 and we report only the two best models. All models including observer effects or weather variables, other than maximum visibility, had no support (Akaike weight = 0). Model-averaged parameter estimates were similar to those in the lowest AIC*c* model.

Our most general model of mean daily counts had an Akaike weight = 1.0, and only this model is reported. The model included significant site ($\beta_{Montclair} = 7.04 \pm 0.10$, $\beta_{Hawk\ Mountain} = 6.26 \pm 0.10$, $P < 0.001$ for both sites, $df_{Montclair} = 1$, $\chi^2_{Montclair} = 5{,}475$, $df_{Hawk\ Mountain} = 1$, $\chi^2_{Hawk\ Mountain} = 3{,}824$), day ($\beta_{day} = 0.02 \pm 0.02$, $P = 0.27$, df = 1, $\chi^2 = 1.20$), and day^2 ($\beta_{day \times day} = -0.02 \pm 0.00$, $P < 0.001$, df = 1, $\chi^2 = 127$) effects, as well as a site × day interaction ($\beta_{Montclair} = 0.06 \pm 0.03$, $P < 0.001$, df = 1, $\chi^2 = 5.46$; Fig. 3). The model suggested that Montclair counts peaked several days later than did those at Hawk Mountain.

Examination of mean cumulative daily proportion of the flight during 1979–1998 also suggested a seasonal difference in the flight between the two sites. Eighty percent of the flight at Hawk Mountain passed by 20 September, whereas 80% of the flight at Montclair had not passed until 22 September. A paired *t*-test on annual median date of the flight also indicated the flight at Montclair lagged that at Hawk Mountain by 2.00 days during 1979–1998 (SE = 0.88, $P = 0.035$, $t = 2.27$, $n = 20$). There was no significant association between total annual counts at the two sites ($P = 0.54$, df = 18, $\chi^2 = 0.37$).

DISCUSSION

Migrating Broad-winged Hawks start to aggregate into large flocks almost as soon as they begin migrating south (Bildstein 1999). As a result, more than half of each year's autumn flight can pass a watch site in 2–4 days, while on many other days during traditional peak passage (i.e., mid- to late September), few birds may be seen (Hawk Mountain Sanc-

TABLE 3. Best model of adjusted daily counts of Broad-winged Hawks at Montclair Hawk Lookout, New Jersey, and Hawk Mountain Sanctuary, Pennsylvania, September 1979–1998.

Parameter	Level	df	Estimate	SE	χ^2	*P*
Site	Montclair	1	0.22	3.97	0.003	0.95
	Hawk Mountain	1	4.48	3.28	1.88	0.17
Site × Day	Montclair	1	0.02	0.02	2.40	0.12
Site × Day	Hawk Mountain	1	0.00	0.01	0.07	0.79
Visibility	Very Hazy	1	−1.42	0.46	9.54	<0.01
	Hazy	1	−0.27	0.28	0.88	0.35
	Clear	1	0.07	0.22	0.10	0.75
	Very Clear	0	0.00	0.00	—	—

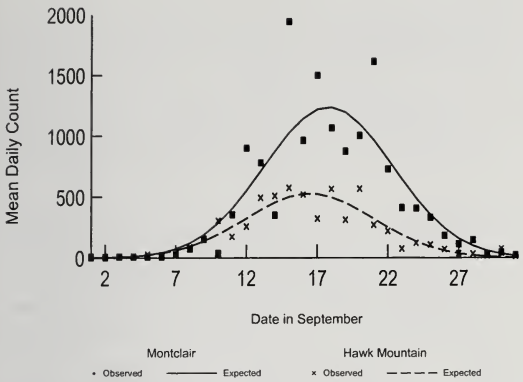

FIG. 3. Mean adjusted daily counts of Broad-winged Hawks observed and expected each September at Montclair Hawk Lookout, New Jersey, and Hawk Mountain Sanctuary, Pennsylvania, 1979–1998.

tuary unpubl. data). Extreme variation in daily counts and, to a lesser degree, marked variation in annual counts at a given site make it difficult to construct explanative models for the flight. Such extreme variation in daily counts may explain why we detected a decreasing trend with annual counts but not with daily counts.

Hawk Mountain is 155 km west-southwest of Montclair. Most Broad-winged Hawks are thought to move generally southwest across the region (Hagar 1988), so we predicted *a priori* that the migration at Hawk Mountain would peak after that at Montclair. That our results were not consistent with this prediction, and annual counts at the two sites were not correlated, suggests that the two watch sites are along different flight corridors, and that birds seen at one site are not likely to be seen at the other. The migration delay along the coast could be due to an ameliorated coastal climate prolonging conditions suitable for thermal generation, thereby permitting later migration times. However, this would not explain the lack of a correlation between annual counts at the two sites.

Broad-winged Hawks counted at Montclair may represent birds traveling south and southwest from eastern New England and the Maritime Provinces of Canada, whereas those passing Hawk Mountain represent birds traveling from Pennsylvania, New York, western New England, Ontario, and Quebec (Fig. 1). Such a scenario makes sense topographically (Kerlinger 1989). Hawks counted at Montclair may alternately slope soar along the ridges of the northern Appalachians and thermal soar and glide across the coastal lowlands to the southeast, whereas hawks counted at Hawk Mountain may primarily slope soar along the ridges of the Adirondack, Catskill, Pocono, and northwestern and central Appalachian mountains (Fig. 1).

Alternatively, birds observed at Montclair may have come from a large northern breeding area and wind drifted toward the coast where they would face the water barrier of Long Island Sound and begin to concentrate (Fogleman 1993). If so, the annual timing and magnitude of the flight at Montclair may be more influenced by the presence or absence of wind drift than the flight at Hawk Mountain. Satellite telemetry could be used to test between these hypotheses.

Another possible explanation for flight differences between the two sites is that adults might comprise most of the flight at Hawk Mountain, while juveniles might comprise most of the flight at Montclair, and that both sites draw upon birds from the same geographic region. However, casual observations have provided no indication that most of the Broad-winged Hawks counted at Montclair are juveniles (EMG and WG pers. obs.). Furthermore, observations at Hawk Mountain suggest that juvenile Broad-winged Hawks migrate earlier, not later than adults (Goodrich et al. 1996).

If regional breeding subpopulations of Broad-winged Hawks exist in the northeastern United Sates and Canada, successful monitoring and conservation efforts on their behalf will depend upon delineating those populations either on the breeding grounds, on the wintering grounds, or in both areas. This may be particularly important given that annual counts at both Montclair and Hawk Mountain appear to be declining. Even upon identification of possible separate populations, monitoring these populations may be possible only by using systematic counts at raptor migration watch sites. Our results suggest that a network of complementary migration watch sites is needed for effective monitoring of populations of this widely dispersed flocking migrant.

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SITE FIDELITY AND LOCAL MOVEMENTS OF MIGRATING WESTERN SANDPIPERS ON THE FRASER RIVER ESTUARY

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ABSTRACT.—The Western Sandpiper (*Calidris mauri*) is the most numerous shorebird on the Pacific coast of North America during spring migration. Twenty-six sandpipers carrying miniature radio transmitters on northward migration across the Fraser River delta, British Columbia, remained on or near to the section of beach where they were first detected through their entire stay. They traveled about 4–6 km each day, following the tide up and down the beach. Although some Western Sandpipers were present on all beaches of the delta, our results suggest that individuals do not roam widely once they settle. The widespread distribution of sandpipers in mud, marsh, and sand habitats suggests that all regions of the Fraser River delta are required to support the large number of Western Sandpipers during spring migration. *Received 19 February 2002, accepted 6 August 2002.*

Conservation programs aimed at protecting migrant shorebirds require information on how species use habitats. Migrating birds might choose among habitats at stopover sites by trading off energetic requirements for continued migration against competitors and avoidance of predators (Metcalfe and Furness 1984, Lindström 1990, Bednekoff and Houston 1994, Clark and Butler 1999, Moore and Aborn 2000, Ydenberg et al. 2002). There are many interacting factors in these decisions, including the fuel loads carried by birds (van Gils and Piersma 1999, Moore and Aborn 2000), their escape maneuverability and the danger from avian predators (Burns and Ydenberg 2002, Ydenberg et al. 2002), the suitability of atmospheric conditions for continued migration, and the position of the individual on the migration relative to other individuals (Butler et al. 1997, Clark and Butler 1999). Moving to a new location might be risky in areas with predatory falcons. Shorebirds also might select particular places to feed that reflect differential prey selection in response to bill and gut morphologies (Sutherland et al. 2000). In either case, there is a paucity of empirical data on the daily movements of individual shorebirds during migration to test these ideas.

The Fraser River delta, British Columbia, supports an abundance of migrant shorebirds, most notably the Western Sandpiper (*Calidris mauri*). The number of sandpipers arriving on the delta increases quickly in late April to a peak number between 100,000 and 500,000 individuals in early May, after which numbers quickly decline, and the migration is largely over by about 10 May (Butler 1994). The time spent by individuals at stopover sites has been estimated for this species (Iverson et al. 1996, Warnock and Bishop 1998), but daily use of habitats by individuals while on migration is unknown. In this paper, we describe how individual Western Sandpipers use habitats on the Fraser River delta during spring migration.

STUDY AREA AND METHODS

Study site.—We conducted field work on the Fraser River delta, British Columbia (49° 10′ N, 123° 00′ W), during spring migration in 1992 and 1995. We examined how individual sandpipers were distributed on the delta during the periods 17 April to 6 May 1992 and 26 April to 14 May 1995. During very low tides, the Fraser River delta has about 22,000 ha of exposed mud and sand beach, about 11,000 ha along the southern shore of the delta (Boundary Bay), 6,000 ha along the southwestern shore (Roberts Bank), and about 5,000 ha along the western shore (Sturgeon Bank; Fig. 1). Boundary Bay and Sturgeon Bank consist of mixed silt and sand whereas Roberts Bank is mostly silt and sand to the south of an industrial jetty and silt and clay to the north. Dense eelgrass beds cover Boundary Bay and the southern portion of Roberts Bank south of the industrial port jetty below about the 1.5- to 2.0-m tide. Eleven sections of the delta (herein "beach section") were designated by nearby road and geographical features (Fig. 1). The width of each beach section at high tide was about 2–6 km.

Tracking.—We studied how Western Sandpipers

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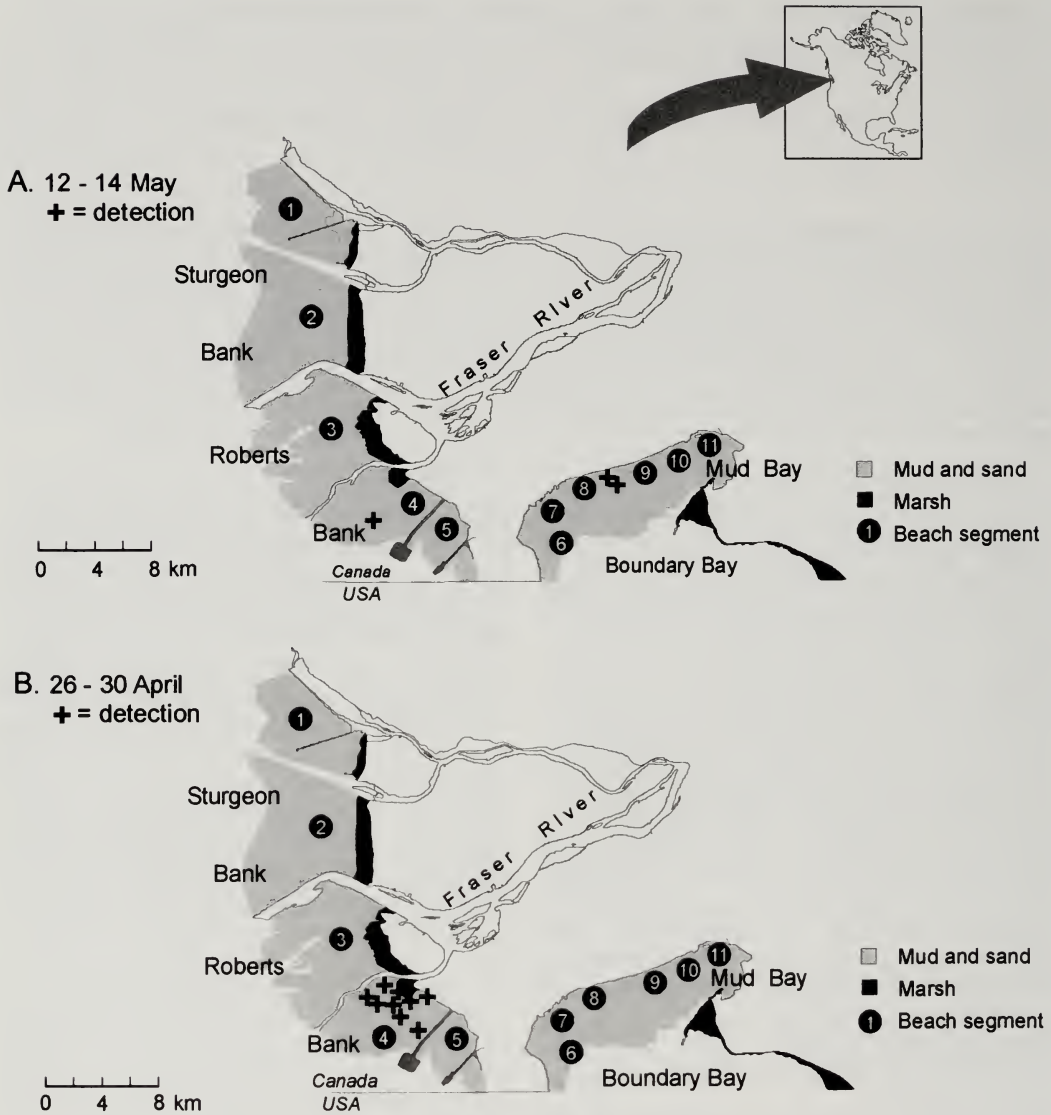

FIG. 1. Detection locations of two radio-marked Western Sandpipers on the Fraser River delta, British Columbia, during 1995.

used the delta by aerial tracking (Iverson et al. 1996) during 1992 (beach sections 1–11) and by ground tracking (Shepherd 2001) of individuals carrying miniature radio transmitters glued to their rump feather tracts (Warnock and Warnock 1993) during 1995 (beach sections 4–11). In 1992, a 0.8-g transmitter (Holohil Systems) was attached to each of four sandpipers caught in California and 11 sandpipers caught on Roberts Bank on the Fraser River delta. The presence of sandpipers carrying transmitters was detected from a Cessna 172 aircraft flown on 18 days for 1.0–1.5 h at about 150 m over the entire intertidal portion of the delta when tides were about 3 m high. Two days of incomplete coverage by aircraft over the delta were excluded from the analysis. We also discarded data from seven transmitters that were heard only once or likely fell off the bird because they were heard repeatedly from one site after the migration was nearly over. We attached a Yagi antenna to the wing strut of the aircraft and used it in connection with an Advanced Telemetry Systems® receiver to detect transmitter frequencies. On 3 May 1992, we flew during a low tide to locate and compare individual movements over the entire exposed beach. We assumed that a radio-marked sandpiper was on the beach below the airplane where the signal was strongest. One observer recorded on a

TABLE 1. Distribution of Western Sandpipers along exposed beach sections of the Fraser River delta, British Columbia, during aerial surveys on 18 days between 17 April and 6 May 1992.

Beach section[a]	Area (%)	Total	Density (birds/ha)
1	105 (4.2)	59,920	571
2	375 (14.9)	42,950	115
3	353 (14.0)	64,950	183
4	244 (9.7)	414,500	1698
5	121 (4.8)	81,620	675
6	36 (1.4)	10,800	300
7	238 (9.4)	55,700	234
8	243 (9.6)	63,920	263
9	291 (11.6)	50,970	175
10	283 (11.2)	85,650	303
11	231 (9.2)	92,900	402
Total	2520 (100.0)	1,023,880	

[a] Sturgeon Banks includes beaches 1–2, Roberts Bank 3–5, and Boundary Bay 6–11.

map the location of each radio-marked bird and estimated the number of sandpipers present on the 11 beach sections. The mean number of days that the 4 sandpipers fitted with radios in California and the 11 sandpipers radio tagged on Roberts Bank were in residence on the Fraser River delta were identical (2.8 days). Therefore, we assumed there was no handling effects on the behavior of birds caught locally and those caught in California.

To estimate the relative density of shorebirds on various beach sections on the delta, we recorded on a map the number and locations of all shorebirds seen during aerial tracking flights during 1992. Aerial surveys can overlook and underestimate the number of birds in large flocks. We assumed that the bias was consistent among days and regions of the delta and use the data only to compare relative use of beach sections by shorebirds.

During 1995, we spent 19 days tracking signals from 0.9-g radio transmitters (Holohil Systems) attached to six sandpipers in San Francisco Bay, three at Honey Lake, California, and two at Grays Harbor, Washington, that remained on the delta for >1 tidal cycle. We tracked sandpipers daily, within 3 h of daytime high and low tides. We examined site fidelity between tidal cycles using detections from these six individuals, which were located hourly between high and low tides. We located sandpipers from 25 telemetry stations along a dike near the high tide line of Boundary Bay and Roberts Bank (covering beach sections 4–11; Fig. 1) with a dual-Yagi van mast telemetry system (Warnock and Takekawa 1995). Two compass bearings were taken from consecutive telemetry stations for all signals. We used these data to triangulate the exact Universal Transverse Mercator (UTM) location for each individual detected on each tracking run. Each location was then plotted on a map of the delta.

RESULTS

Sandpipers used all regions of the delta, but were most numerous on Roberts Bank (beach section 4 in Fig. 1). Over two-fifths of all sandpipers were counted there and they were more dense there than at any other section of beach (Table 1). Most sandpipers carrying radio transmitters were relocated each day on the same beach section. The 1992 aerial surveys detected 15 sandpipers with radios on 53 occasions over 18 days of the migration. Of the 53 detections, 8 were made in Boundary Bay, 42 were made on Roberts Bank and 3 were made on Sturgeon Bank. Of 38 detections on subsequent days following the first detection, 33 (87%) were on the same or adjacent beach section (Table 2). During 1995, we detected 11 individuals on 52 occasions separated by tidal cycles and 41 on subsequent days. Of the 52 detections, 10 were made in Boundary Bay and 42 were made on Roberts Bank. Of 41 detections on subsequent days following the first detection, 33 (80%) were on the same or adjacent beach section; the distance between detections in 1992 and 1995 were not significantly different (Table 2).

On average, each beach section covered about 9% of the entire exposed area and each sandpiper stayed for about 3 days (Iverson et

TABLE 2. Relative movement of 26 radio-marked Western Sandpipers detected two or more times on the Fraser River delta, British Columbia, during spring migration. Values do not include first detection. Beach segments are illustrated in Figure 1.

Year[a]	*n*	Total number of detections	Same beach	Adjacent beach	Two beaches away	Three beaches away	Four beaches away	Five beaches away
1992	15	38	19	14	3	2	0	0
1995	11	41	24	9	2	0	5	1
Total	26	79	43	23	5	2	5	1

[a] Difference between years of the number detected on same, 1, 2, and >2 beaches away was not significant ($\chi^2 = 2.3$, df = 2, $P = 0.34$).

al. 1996). Thus, the probability of a sandpiper randomly selecting the same beach section for three consecutive days is about $0.09^3 = 0.0007$. However, we found 43 of 79 detections (0.54) were made on the same section of beach (Table 2). The UTM coordinates showed that most individuals moved about 4–6 km during stopover, traveling about 2–3 km each way as they moved out and back with the tide. This pattern of movement was confirmed by our observations of flocks on the beach and by tracking six individuals in those flocks through tide cycles. In all cases, the flocks and radio-marked sandpipers followed the tide on the same beach section. The maximum straight-line distance between detections of an individual was 20 km. In 1995, migrants that arrived late in the migration (4–12 May) moved slightly but significantly farther than individuals present early in the migration (26–30 April); 21 detections were made on the same or adjacent beach and two on more distant beaches among early migrants versus 12 and 6 detections, respectively, among late migrants ($\chi^2 = 3.9$, df = 1, $P = 0.049$). We had too few data for late migrants for a comparison in 1992.

DISCUSSION

At least some shorebirds return to the same beach on successive migrations, and during successive breeding and nonbreeding seasons (reviewed by Evans and Townshend 1988, Smith and Houghton 1984, Harrington et al. 1988, Pfister et al. 1998, this study). Individual Western Sandpipers in San Francisco Bay and Dunlins (*Calidris alpina*) on the Fraser River estuary held small winter home ranges and seldom mixed with other sandpipers (Warnock and Takekawa 1995, Shepherd 2001). Our study extends their conclusion to include a stopover site on spring migration. In addition, our study is among the first to examine within-site affinity at a stopover site of any shorebird on migration. Van Gils and Piersma (1999) showed that Red Knots (*C. canutus*) traveled a mean of about 20 km during a tidal cycle in the Dutch Wadden Sea during southward migration. Our study showed that individuals traveled less widely while on the Fraser River delta, with most birds moving no farther than a few kilometers over successive days. However, we do not know if they wandered briefly before we first detected them.

The characteristic pattern of use by individual Western Sandpipers was to follow the tide down and up the beaches through a tidal cycle. Birds seldom settled in nearby fields during high tide, choosing instead to roost along the shore or fly offshore in large flocks. Although flocks used all exposed beach sections on the delta, hundreds of thousands of individuals massed on Roberts Bank during late April and early May. Fewer than 10,000 shorebirds were present on Roberts Bank from 16–24 April 1995. The numbers suddenly increased to about 70,000 on 25 April and to 350,000–500,000 between 26 and 30 April. Fewer than 100,000 were present on 1 and 3 May. At the same time, flocks of hundreds or a few thousand were present on several of the remaining beach sections. These observations led us to believe that sandpipers would follow each other to new locations between successive high tides. We were surprised to discover that they instead returned to the same section of beach on successive low tides.

We believe the reason for the strong affinity to particular beaches by Western Sandpipers was the experience they gained on the previous low tide. The risk of being caught by falcons might be too great to move from a familiar to an unfamiliar location (Ydenberg et al. 2002). The main predators of sandpipers on the Fraser River delta are Peregrine Falcons (*Falco peregrinus*) and Merlins (*F. columbarius*) that hunt mostly by surprise (Dekker 1995, 1998; Butler 1999). The sandpipers clearly were alarmed by the presence of falcons and quickly took evasive flight action. Thousands formed into large flocks over the ocean where they were pursued by falcons. Similar over-ocean flocking has been reported among Dunlins in the presence of falcons in our study area and in Europe (Dekker 1998, Hötker 2000).

Sutherland et al. (2000) suggested that Western Sandpipers might select habitats that are most suited to their bill morphology and dietary preferences. However, Lissimore et al. (1999) found no differences in culmen lengths in Western Sandpipers between the estuarine mudflats on the Fraser River estuary and a nearby lagoon on Sidney Island. However, they did find significant and consistent differ-

ences in body mass. This suggests that body mass might be a more important factor than structural size in site choice by birds at stopover sites (Van Gils and Piersma 1999, Moore and Aborn 2000).

A conservation message arising from our study is that the beaches of the entire Fraser River delta are important to shorebirds. They used all the beaches during the entire migration and individuals mostly did not move to other beaches once they had settled. Western Sandpipers were rarely seen or heard in nearby farm fields, which are used by Dunlins and Black-bellied Plovers (*Pluvialis squatarola*) during winter and spring (Butler 1999) These results suggest that Western Sandpipers have strong affinities for particular beaches on the Fraser River delta and that these mudflats are irreplaceable.

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THE BIRDS OF ST. MATTHEW ISLAND, BERING SEA

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ABSTRACT.—St. Matthew Island (60° 24′ N, 172° 42′ W) and its small nearby satellites, Hall Island and Pinnacle Rock, are isolated in the northcentral Bering Sea. This infrequently visited location occupies a geographic position with a deep Bering Land Bridge history and is in an area of interdigitation of the Old World, New World, and Beringian avifaunas. It is known for its three Beringian endemics, a bird (McKay's Bunting, *Plectrophenax hyperboreus*), a small mammal, and a plant. This level of endemism is striking for a high-latitude island. The only previous summary of the avifauna of St. Matthew island (Hanna 1917) included 37 species. Our report considers more than 125 species and synthesizes data on presence and absence, abundance, and phenology. Because visits have been infrequent and concentrated during summer, our understanding of migration in this region remains poor, but the area is clearly affected by both the Old and New world migration systems. There is sufficient evidence to show that some profound changes among the island's breeding birds have occurred during the past century. In particular, the breeding range of Glaucous-winged Gulls (*Larus glaucescens*) has been extended north to include St. Matthew, a change that is correlated with a northward shift in the extent of sea ice (Maslanik et al. 1996). King and Common eiders (*Somateria spectabilis* and *S. mollissima*) also have shown substantial changes in summer abundance. Other changes in the summer avifauna (e.g., among shorebirds) may reflect the dynamics of edge-of-range phenomena. Because of its central position in a region undergoing profound climate change and its demonstrated track record in showing avifaunal shifts, St. Matthew Island may represent an important bellwether for monitoring the biological effects of further climate change in the northern Bering Sea. *Received 31 July 2001, accepted 15 April 2002.*

Isolated in the northcentral Bering Sea at 60° 24′ N, 172° 42′ W, St. Matthew Island and its small nearby satellites, Hall Island and Pinnacle Rock, occupy a central geographic position relative to the breeding ranges and seasonal movements of the different bird faunas to the north (St. Lawrence Island and Bering Strait), south (Pribilof and Aleutian islands), east (the Alaska mainland), and west (Kamchatka, the Koryak Highlands, Gulf of Anadyr, and Chukotsk Peninsula). This position (Fig. 1) provides a unique perspective on the dynamic and complex interdigitation of the northern Palearctic and Nearctic avifaunas and of both of these with the endemic Beringian avifauna. The phenologies of events such as reproduction, migration, and overwintering status in this region are poorly known. Further, this region is likely to undergo greater than average responses to global warming (Myneni et al. 1997), suggesting that the timing of these events may change in the future.

St. Matthew Island (including Hall Island and Pinnacle Rock) is perhaps most noteworthy biologically for constituting the home of an endemic mammal (St. Matthew Island vole, *Microtus abbreviatus*), an endemic plant (*Artemisia globularia* var. *lutea*), and the entire breeding range of a species of bird (McKay's Bunting, *Plectrophenax hyperboreus*). In addition, the nominate subspecies of the Rock Sandpiper (*Calidris ptilocnemis ptilocnemis*) breeds only here and on the Pribilof Islands, as does a subspecies of the Gray-crowned Rosy-Finch (*Leucosticte tephrocotis umbrina*). This level of endemism is surprising for a small land area at such a high latitude, but no doubt reflects the deep temporal history of a once larger Beringia.

These islands were an unglaciated refugium during past ice ages (Hamilton et al. 1986). Pollen sequences from St. Lawrence Island

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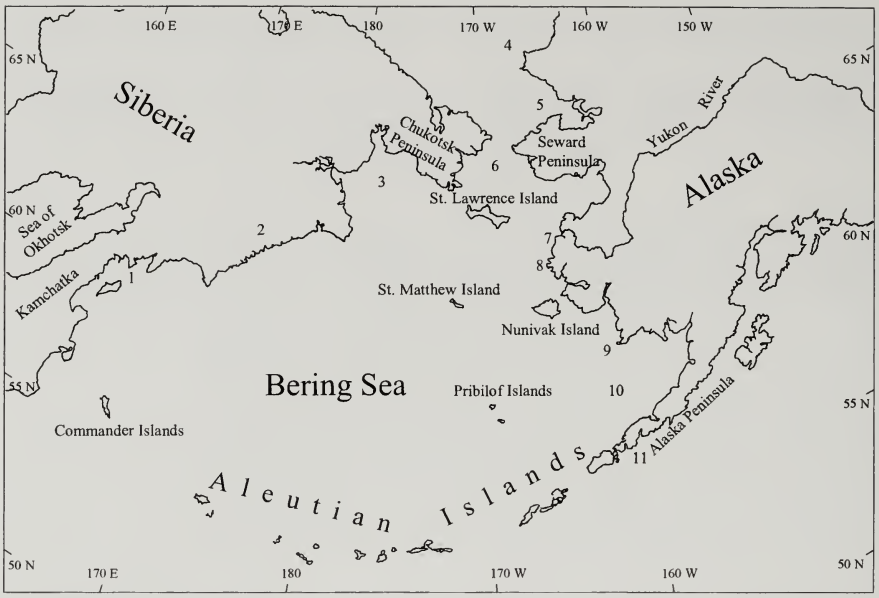

FIG. 1. St Matthew Island (center) and the greater Beringian region, including most locations mentioned in the text. Numerical locations are (1) Karaginskiy Bay, (2) Koryak Highlands, (3) Gulf of Anadyr, (4) Cape Lisburne, (5) Kotzebue Sound, (6) Bering Strait, (7) Yukon-Kuskokwim Delta, (8) Cape Romanzof, (9) Cape Newenham, (10) Bristol Bay, and (11) Shumagin Islands.

and the Pribilof Islands, to the north and south, respectively, reveal a very long unglaciated history for the region (30,000–70,000 years), with full-glacial records suggestive of xeric tundra with some indication (from an unknown source) of spruce, birch, and alder (Barnosky et al. 1987). The islands have been protected since the Bering Sea Bird Reservation was established in 1909, and they are presently contained within the Alaska Maritime National Wildlife Refuge.

Avian study has been conducted only sporadically, and usually briefly, at this remote locality. No summary of the avifauna of this island group has appeared in the ornithological literature since Hanna (1917). The first ornithological venture on these islands may have been that of von Kittlitz, who took a few specimens there in the mid-1800s (Rausch and Rausch 1968). The islands first came to prominent ornithological attention when Hall Island was discovered to be the breeding ground of McKay's Bunting (Ridgway 1886, Townsend 1887). Albert K. Fisher and others visited on 14–15 July 1899 as part of the Harriman Expedition (Goetzmann and Sloan 1982), but their ornithological observations were never published. During 8–13 July 1916, G. Dallas Hanna visited under the aegis of the U.S. Biological Survey; his published report (Hanna 1917), which included A. K. Fisher's notes from 1899, summarized the 37 species then known from the islands. Ira N. Gabrielson was the next ornithologist to visit, briefly, on 8–9 July 1940 (Gabrielson 1944), and he visited briefly again on 7 August 1946 (Gabrielson and Lincoln 1959). The unpublished notes of Frank L. Beals (copy at Univ. of Alaska Museum) were an invaluable source of additional information. Beals was at St. Matthew with the U.S. Fish and Wildlife Service from 24 June to 16 August 1944. His notes include a wealth of useful information, including the notes of Russell V. Anderson, who was on the island with the U.S. Coast Guard from July 1943 to June 1944 and was able to provide glimpses of phenology that could be gathered only by someone on the island throughout the year. Detlef Eisfeld visited the island from 30 June to 20 July 1966 and also made important avian observations. For Klein (1959) in 1957 and Rausch and Rausch (1968) in 1954, a look at St. Matthew's birds was peripheral to their work on mammals. More recently, in response

to projected development of the island as a logistical base for offshore oil exploration in the Navarin Basin oil and gas lease area, fieldwork conducted in the 1980s produced much useful information on five species of cliff-nesting seabirds (Murphy et al. 1987), but only sketchy information on most other avian species.

Hanna's (1917) report considered 37 species; we include 125 and also discuss the status of four others. Our purpose in this study has been to survey and update baseline information on the St. Matthew Island avifauna because of its importance to our understanding of broader regional topics such as Beringia, the crossover of continental avifaunas, and the biological effects of climate change.

METHODS

Study area.—St. Matthew Island comprises some 470 km^2 (52 × 9 km) of rolling subarctic tundra (elevations to 430 m) with freshwater lakes and streams, gently sloping beaches, and precipitous seacliffs. With its two satellites, Hall Island (9 × 3 km) and Pinnacle Rock, St. Matthew is "barren, treeless, uninhabited and surrounded by dangerous and poorly charted waters" (Hanna 1917:403).

Methods.—In the species accounts below, phylogenetic sequence and scientific and English names follow AOU checklist (American Ornithologists' Union 1998), subspecies nomenclature follows Gibson and Kessel (1997), and status and abundance terminology follow Kessel and Gibson (1978). We summarize existing phenological information while recognizing that it is incomplete. Unattributed data are those of the authors. "UAM unpubl." refers to unpublished Alaska bird records archived at the Univ. of Alaska Museum. Parenthetical subspecific names indicate a subspecies that is inferred by range; parenthetical "ssp." indicate that it is unreasonable to infer subspecies without specimens. Taxa in square brackets we consider to be unsubstantiated records. The complex zoogeography of the avifauna in this region often requires reference to broader regional status to place existing data in context. Where necessary, we include brief summaries.

In the past, midsummer occurrences of many species at northerly latitudes were inferred to represent breeding simply because of presence at that season. We now know that midsummer occurrences in this region regularly include late-migrant stragglers, nonbreeding birds summering just beyond the limits of the breeding range, and early returning failed breeders. Such birds can complicate an assessment of avian status during the breeding season, and presence alone cannot be inferred to be evidence of breeding (e.g., see Johansen 1961, versus American Ornithologists' Union 1957). Where we have no more than circumstantial evidence, therefore, we have been conservative about attributing breeding status to various species on these islands.

ANNOTATED SPECIES LIST

Gavia stellata (Red-throated Loon). Fairly common breeder. Numerous and nesting in 1916 (Hanna 1917). High counts have included four pairs with six young (July 1944, F. L. Beals). Several nests and adults with young in summer 1982, maximum day count of six (7 June). The only common nesting loon in the Aleutians (Murie 1959), at Nunivak Island (Swarth 1934), and at St. Lawrence Island (Fay and Cade 1959).

Gavia arctica (*viridigularis*) (Arctic Loon) or *G. pacifica* (Pacific Loon). Rare in spring and summer. "Arctic" loons occurred from 28 May (1982) to 5 July (1977), usually singly, maximum three (DeGange and Sowls 1978). In Asia, *arctica* and *pacifica* breed in sympatry from Chukotsk Peninsula to the Koryak Highlands (Kishchinskii 1980), but *arctica* alone breeds in Kamchatka and the Sea of Okhotsk (Vaurie 1965). The latter nests at St. Lawrence Island (Fay and Cade 1959) and on the entire Bering coast of the Alaska mainland (Gabrielson and Lincoln 1959), while the former breeds in Alaska only on the Seward Peninsula and in Kotzebue Sound (Douglas and Sowl 1993). Both have been recorded on migration in the Pribilofs (Preble and McAtee 1923, Sladen 1966), and both occur in winter in the Aleutians (UAM unpubl. data).

Gavia immer (Common Loon). Casual in spring and summer. Single adults on ocean 27 to 29 May and 1 June 1982; two on fresh water on 19 June 1982. This primarily New World species nests locally in the Aleutians (Murie 1959), but not in the Commander Islands nor on islands in the Bering Sea. There are a few records at St. Lawrence Island (Fay and Cade 1959; UAM unpubl. data), but it is apparently unknown on Chukotsk Peninsula (Portenko 1973).

Gavia adamsii (Yellow-billed Loon). Rare in spring. One on 2 June 1982. Breeds as far south in Alaska as the Seward Peninsula (Kessel 1989) and St. Lawrence Island (Fay and Cade 1959), and it is a widespread breeder on the Chukotsk Peninsula (Portenko 1973).

Podiceps grisegena (*holboellii*) (Red-necked Grebe). Rare in spring and casual in summer. Singles seen 27 May through 14 June

1982 and on 26 June 1982; maximum seen was two (28 May 1982 and 5–6 July 1985). Has nested at St. Lawrence Island (Sealy et al. 1971).

[*Phoebastria nigripes* (Black-footed Albatross)]. Two reported offshore on 15 July 1957 (Klein 1959).

Fulmarus glacialis rodgersii (Northern Fulmar). Abundant breeder. Made up mostly of light morph birds, the breeding population was estimated at 450,000 birds in 1977 (DeGange and Sowls 1978, Sowls et al. 1978). Recorded as early as about 1 May (1944, R. V. Anderson *fide* F. L. Beals). Many pairs by 22 May 1982, first egg laid 1 June, and first chick seen 21 July. In 1985 earliest chick (<1 one week old) seen 27 July; earliest unattended chicks 2 August (1986).

Puffinus tenuirostris (Short-tailed Shearwater). Common in summer. Noted by 31 May (1982); maximum count was 6,000+ (18 June 1982).

Oceanodroma furcata (*furcata*) (Fork-tailed Storm-Petrel). Casual in summer. One on 4 June 1982, two on 24 July 1983, four on 8 August 1983, and one 18 km east of St. Matthew on 21 August 1985. Species does not nest north of the Aleutian (Sowls et al. 1978) and Commander (Kondratyev et al. 2000) islands.

Phalacrocorax auritus (*cincinatus*) (Double-crested Cormorant). Casual or accidental in summer. One seen 21 June 1982. Not known to nest closer than Cape Newenham southeastern Bering Sea (Petersen et al. 1991) and the eastern Aleutians (Sowls et al. 1978).

[*Phalacrocorax urile* (Red-faced Cormorant)]. Attributed, apparently erroneously, to St. Matthew by Nelson (1887). Kessel and Gibson (1994) discussed confusion in published historical accounts of cormorant distributions in Alaska. There have been only scattered records north of the Pribilofs (UAM unpubl. data).

Phalacrocorax pelagicus pelagicus (Pelagic Cormorant). Common breeder, uncommon at other seasons. Arrived as early as about 15 May (1944) and departed before September (1943; both dates R. V. Anderson *fide* F. L. Beals). In 1977 estimated nesting population was 3,000 (DeGange and Sowls 1978). Breeding phenology included birds carrying nesting materials on 1 June (1983) and 6 June (1982); birds first at nests on 8 June (1982); first eggs on 13 June, first chicks 3 July, and downy chicks and young two-thirds adult size seen by 29 July 1982. Also recorded in midwinter: on 6–7 February 1970, McRoy et al. (1971: 64) noted "one small flock flying offshore."

Anser fabalis (*serrirostris*) (Bean Goose). Casual in summer. One present 17–23 June 1982. Rare in spring in the Aleutians and casual in spring on Bering Sea islands (Kessel and Gibson 1978). Breeds east to Gulf of Anadyr and Chukotsk Peninsula (Vaurie 1965).

Anser albifrons (*frontalis*) (Greater White-fronted Goose). Casual in spring. Two seen with a Canada Goose 24–26 May 1982, and one with six Brant 7–11 June 1982. Casual migrant at St. Lawrence Island (Johnson 1976; UAM unpubl. data).

Chen canagica (Emperor Goose). Casual in summer. Small numbers 4–20 June 1982, and at least two on 8 July 1985 (G. V. Byrd pers. comm.). It is possible that annual movements largely bypass St. Matthew Island. Species is (or was, see Kessel and Gibson 1994 and citations therein) a widespread breeder at St. Lawrence Island (Fay and Cade 1959) and the Yukon-Kuskokwim Delta (King and Dau 1981), and it probably performs a midsummer molt migration from the Y-K Delta to St. Lawrence Island (Jones 1972). Winters throughout the Aleutians (Murie 1959).

Chen caerulescens (*caerulescens*) (Snow Goose). Casual in spring. Up to 57 seen 22 May through 7 June 1982. Main migration in western Alaska probably bypasses St. Matthew Island; nearest breeding is at Wrangel Island, Chukchi Sea (King and Dau 1981).

Branta canadensis (ssp.) (Canada Goose). Casual in spring. Flock of 20–30 with Snow Geese 22–24 May 1982; four birds on 15 July 1982. Numerous on Bering coast of mainland Alaska (King and Dau 1981), where *B. c. minima* breeds and *parvipes* (including *taverneri*) is a migrant, but only of casual occurrence at St. Lawrence Island (see Sealy et al. 1971). A 1903 specimen of *B. c. occidentalis* from Gulf of Anadyr seems to be the only record of this species in northeasternmost Asia (Dementiev and Gladkov 1952, Vaurie 1965).

Branta bernicla (*nigricans*) (Brant). Rare in summer. Up to six seen 6–23 June 1982; two on 11 June 1986 (K. D. Schafer pers. comm.).

Occurs regularly in spring and summer at St. Lawrence Island (Sealy et al. 1971).

Cygnus columbianus (*columbianus*) (Tundra Swan). Uncommon in summer; possible breeder. Hanna (1917:408) saw 2–4 swans on lakes "at every landing place" in July 1916. Klein (1959) reported two seen in July and August 1957. One on 9 July 1966 was nesting (D. Eisfeld pers. comm.). Thirteen swans in summer 1977 (DeGange and Sowls 1978) were likely this species. During 1980s swans seen only erratically and in small numbers, maximum five on 3 August 1982. One seen 11 June 1986 was identified (K. D. Schafer pers. comm.) as *C. c. bewickii*, the Old World subspecies, known in Alaska from only one record (Evans and Sladen 1980).

Anas penelope (Eurasian Wigeon). Rare in spring. Hanna (1917) identified wings nailed to the wall of a derelict cabin. Seen 26 May to 13 June 1982, maximum seven on 31 May. Rare in spring on Bering Sea islands (Kessel and Gibson 1978).

Anas americana (American Wigeon). Casual in spring. Up to four with Eurasian Wigeon 26 May through 4 June 1982; another pair on 1 June 1982. Casual in spring on Bering Sea islands (UAM unpubl. data).

Anas platyrhynchos (*platyrhynchos*) (Mallard). Rare in spring and summer. Pair seen 8 July 1916 (Hanna 1917). One male seen 28–29 May 1982, one bird on 10–12 July 1982, and another male seen 6 July 1985. Also rare at St. Lawrence Island (Sealy et al. 1971).

Anas clypeata (Northern Shoveler). Casual in spring. A pair was seen 1–3 June 1982. Casual in spring at St. Lawrence Island (Fay and Cade 1959; UAM unpubl. data).

Anas acuta (Northern Pintail). Uncommon or fairly common migrant; rare in summer, when possibly rare breeder. Klein (1959) reported 15 birds, which he said bred. Frequently observed in summer 1977 (DeGange and Sowls 1978). Present by 22 May 1982, up to 70 per day until 30 May, after which singles or groups of up to seven periodically mid-June to early 6 August. Lone male seen twice in July 1966 (D. Eisfeld pers. comm.); up to 10 on 5–6 July 1985; 10 flightless adults on 22 July 1997. During 9–12 August 1985 scattered birds seen, maximum a flock of 40+. No suggestion of nesting during our fieldwork.

Anas crecca (*crecca* and *carolinensis*) (Green-winged Teal). Rare migrant (both subspecies) and in summer. Hanna (1917) identified wings nailed to the wall of a derelict cabin. Species seen 23 May (1982) to 8 June (1982), sometimes paired, always few. Agonistic behavior between these forms seen 2 June 1982, when a male *carolinensis* chased an apparently paired male *crecca*, and the *carolinensis* flew off with the female. Summer records included a pair on 13 July 1985, three on 22 July 1986, four on 22 July 1997, and one 9 August 1985. Both subspecies are rare in spring and summer at St. Lawrence Island (UAM unpubl. data), where Sealy et al. (1971) suspected breeding.

Aythya ferina (Common Pochard). Casual in summer. Male seen 6–12 June 1982. Species is rare in spring in western Aleutians and casual in spring in the Pribilofs (Kessel and Gibson 1978); there is one record from St. Lawrence Island (UAM unpubl. data).

Aythya fuligula (Tufted Duck). Casual in summer. Male seen 3 July 1977 (DeGange and Sowls 1978). Species is very rare or casual north of the Aleutians, where it occurs in small numbers at any season (Kessel and Gibson 1978).

Aythya marila (ssp.) (Greater Scaup). Uncommon in spring and rare in summer. Reported 1 June 1944 (R. V. Anderson *fide* F. L. Beals); three noted in summer 1977 (DeGange and Sowls 1978). In subsequent years from 27 May (1982) to 6 July (1985), maximum 10 on 9 June 1983.

Polysticta stelleri (Steller's Eider). Uncommon in summer; nonbreeder. In 1977 five in basic plumage were seen on 30 June, 152 birds accompanied by two King and several Common eiders on 13 July, and five on 14 July (DeGange and Sowls 1978). A male on fresh water on 3 June was the only sighting in 1982. On 8 June 1983 a flock of 80+ (mostly females, a few immature males) was first sighting of that summer, after which groups of 25 and 10 on 23 June and 25 June, respectively; species also noted on 3 and 5 July.

Somateria spectabilis (King Eider). Rare in summer; uncommon in winter. If Hanna's (1917) report accurate (abundant; evidently nesting), there has been a substantial change in status since 1916. Not seen by Gabrielson (1944) in July 1940 visit. DeGange and Sowls

(1978) saw two in summer 1977. In 1982 two on 4 June on fresh water. Not recorded summers 1983, 1985, or 1997. Identified in midwinter by McRoy et al. (1971:63), who on 6–7 February 1970 noted it and Common Eiders "in fair numbers, feeding in the open leads and flying restlessly back and forth, sometimes resting on the edge of the ice."

Somateria mollissima v-nigrum (Common Eider). Common breeder; uncommon in winter. Not recorded by Gabrielson (1944) on 8–9 July 1940. Nesting reported by Beals in 1944 and by Klein (1959), and an incubating female found 2 July 1966 (D. Eisfeld pers. comm.). In June and July 1977, when nested, paired on lakes and beach strands, also in rafts of 50–100+ offshore (DeGange and Sowls 1978). No evidence of breeding in 1982 or 1983, but paired birds seen, sometimes in lakeshore vegetation, and copulation on the ocean seen 15 June. Frequent in May and June 1983. Flocks of 22 on ocean 3 July 1985, of 16 on fresh water next day. Common breeder in July 1997, when young were seen. Reported in midwinter by McRoy et al. (1971), on 6–7 February 1970 (see King Eider).

Histrionicus histrionicus (Harlequin Duck). Fairly common throughout year; nonbreeder. Hanna (1917) saw a small flock 13 July 1916. Only on salt water, maxima 350–400 on 2 August 1944 (F. L. Beals) and 200 in June to July 1977 (DeGange and Sowls 1978). With murres and Long-tailed Ducks, Harlequins were the most numerous birds observed 6–7 February 1970 (McRoy et al. 1971).

Melanitta perspicillata (Surf Scoter). Casual in spring and summer. Four on 31 May 1982 and flock of 25 on 22 July 1997. Species is casual in spring at St. Lawrence Island (UAM unpubl. data), accidental on Chukotsk Peninsula (Portenko 1973).

Melanitta fusca (ssp.) (White-winged Scoter). Casual in spring and summer. In 1982 two were seen 27 May, four on 31 May, seven on 11 June, and up to nine 8–15 June. A casual migrant at St. Lawrence Island (Sealy et al. 1971).

Melanitta nigra (*americana*) (Black Scoter). Casual in spring and summer. A male was seen 28 May 1982, and one bird on 9 June 1983. A casual migrant at St. Lawrence Island (Sealy et al. 1971).

Clangula hyemalis (Long-tailed Duck). Common throughout the year. A very few nested in 1916 (Hanna 1917). Fledged young seen at end of July 1944 (F. L. Beals pers. comm.), in 1957 (Klein 1959), and in 1966 (D. Eisfeld pers. comm.). In 1982 copulation noted 28 May, courtship and territory defense 2 June, but no nests or young seen. In 1983 pairs in courtship and copulation on 5 June. Species present all winter 1943–1944 (R. V. Anderson *fide* F. L. Beals). With murres and Harlequin Ducks, Long-tailed Ducks were the most common birds seen 6–7 February 1970 (McRoy et al. 1971).

Bucephala albeola (Bufflehead). Casual in spring and summer. Up to three pairs seen 28 May to 4 June 1982. Two present 4–9 June 1983. Casual spring migrant at St. Lawrence Island (UAM unpubl. data).

Bucephala clangula (ssp.) (Common Goldeneye). Casual in spring and summer. Five to eight were present during July 1966 (D. Eisfeld pers. comm.), up to four 28 May to 16 June 1982, a pair on 9 June 1983, and two on 11 June 1986 (K. D. Schafer pers. comm.). Casual in spring at St. Lawrence Island (UAM unpubl. data).

Bucephala islandica (Barrow's Goldeneye). Casual or accidental in spring. Pair seen 2 June 1982. Casual in spring on coast of mainland western Alaska; unknown at St. Lawrence Island (UAM unpubl. data).

Mergus serrator (Red-breasted Merganser). Uncommon migrant and in summer. Reported as early as about 20 May (1944, R. V. Anderson *fide* F. L. Beals). DeGange and Sowls (1978) observed three in 1977. Up to three present 2 June to 12 July 1982, a pair on 15 June 1983, six on 11 July 1986. Possible breeder at St. Lawrence Island (Sealy et al. 1971).

Circus cyaneus (ssp.) (Northern Harrier). Casual or accidental in spring. Female seen 23–25 May 1982. Species is apparently unknown at St. Lawrence Island.

Grus canadensis (*canadensis*) (Sandhill Crane). Rare or uncommon migrant and in summer; possible breeder. One seen 8–12 July 1916 by Hanna (1917, who did not report the species to be nesting cf. Gabrielson and Lincoln 1959:315); pair on 9 July 1940 inferred to be "evidently nesting" (Gabrielson 1944: 122) from midsummer presence. Recorded in small numbers in summer 1977 (DeGange and

Sowls 1978). Present by 22 May (1982) and through at least 12 June (1983). Not clear if birds present continuously from mid-June to mid-July, but many sightings from 6 July (1985) to 20 July (1997), maximum a flock of 50 on 18 July 1997. Seven on 3 August 1982 and at least 10 present 14–19 August 1985 were the only late-summer records. Maximum count in spring was flock of 70+ (22 May 1982).

Regular occurrence at St. Matthew probably represents the southern edge of annual movement between Alaska mainland and Chukotsk Peninsula; the bulk of this passage crosses the Bering Strait and northern Bering Sea from the Seward Peninsula and St. Lawrence Island to the Chukotsk Peninsula (Kessel 1984). Breeds on Alaska mainland coast (Brandt 1943, Gabrielson and Lincoln 1959, Shields and Peyton 1979, Woodby and Divoky 1983, Kessel 1989, Petersen et al. 1991), at St. Lawrence Island (Fay and Cade 1959, Sauer and Urban 1964), and at Nunivak Island (Swarth 1934) and breeds in northeastern Siberia in the Gulf of Anadyr (Vaurie 1965). In the Bering Sea south of St. Matthew only casual in the Pribilofs (Preble and McAtee 1923) and Aleutians (Byrd et al. 1974).

Pluvialis fulva (Pacific Golden-Plover). Common migrant; casual in midsummer, possible rare breeder. Conspicuous by 22 May 1982 and present through 6 June. Pair seen 30 June to 20 July 1966 "behaved as if breeding" (D. Eisfeld pers. comm.), and a pair on 4 July 1985 acted territorial. Earliest postbreeding migrants seen 18 July 1982, 19 and 24 July 1997, and 27 July 1944 (F. L. Beals pers. comm.), after which dates southbound individuals plentiful through observers' mid- and late-August departures. Species breeds at St. Lawrence Island (Fay and Cade 1959) and at Nunivak Island (Swarth 1934).

Charadrius mongolus (*stegmanni*) (Mongolian Plover). Casual in spring. Three or four seen 23 May to 3 June 1982. Rare migrant in the Aleutians and at St. Lawrence Island; species has nested on the Alaska mainland (Kessel and Gibson 1978).

[*Charadrius hiaticula* (Common Ringed Plover)]. Identified on 8 and 12 June 1982, including a bird at nest with two eggs. Both Palearctic *hiaticula* and Nearctic *semipalmatus* have nested at St. Lawrence Island (Sealy et al. 1971), so their distributions in the Bering Sea warrant close scrutiny. In the absence of substantiation, therefore, this species must be regarded as unconfirmed at St. Matthew. In Alaska south of St. Lawrence Island, *C. hiaticula* is known with certainty only as a casual migrant in the western Aleutians (see Byrd et al. 1978). *Charadrius semipalmatus* breeds as far west as the eastern Aleutians and the Pribilofs (UAM unpubl. data) and at St. Matthew (this paper).

Charadrius semipalmatus (Semipalmated Plover). Rare breeder. First recorded 1977, when species nested in small numbers (downy chick seen 14 July, DeGange and Sowls 1978). No arrival or departure information. Recorded 19 June 1982, and two adults seen with chick on 2 July 1982. First sighting in 1983 on 23 June; on 3 July pair observed in distraction display, but no young found; one adult seen 21 July. Pair at nest with two eggs 3 July 1985. One adult on 23 July 1985, an adult and two juveniles on 7 August, and an adult on 10 and 13 August. Two observed 9 July 1986. Adult female and downy chick (UAM 7743 and 7744) documented breeding 22 July 1997, when four adults seen.

Charadrius morinellus (Eurasian Dotterel). Casual or accidental in spring. One seen 28 May 1982. A trans-Bering Strait migrant to the Seward Peninsula and St. Lawrence Island (Kessel and Gibson 1978), but south of there known in Alaska only in fall in the western Aleutians (Gibson 1981).

Heteroscelus incanus (Wandering Tattler). Uncommon migrant. Reported by Beals (in 1944), Klein (1959), and DeGange and Sowls (1978). Present by 29 May (1982), spring maximum three on 2 June 1982. Earliest postbreeding migrants seen 22 July (1986), 25 July (1985), 29 July (1957, Klein 1959), and 2 August (1944, F. L. Beals), maximum four on 10 August 1986. Many tattlers were identified only to genus.

Heteroscelus brevipes (Gray-tailed Tattler). Rare migrant. Lone birds seen at intervals 29 May to 16 June 1982. Two seen 2–4 June 1983. Earliest postbreeding arrivals seen 25 July and 8–9 August 1983. Rare migrant on Bering Sea islands (Kessel and Gibson 1978).

Actitis hypoleucos (Common Sandpiper). Casual in spring. Two birds seen 7–9 June

1982. Very rare spring migrant on Bering Sea islands (Kessel and Gibson 1978).

Numenius phaeopus (*variegatus*) (Whimbrel). Rare migrant. Reports without details in August 1954 (Rausch and Rausch 1968), of an unidentified curlew on 1 June 1982, and of a Whimbrel 18 August 1985 are recorded tentatively as this taxon, a rare or uncommon migrant in the western Aleutians (Gibson 1981) and at St. Lawrence Island (ibid.; UAM unpubl. data). Both Asiatic *variegatus* and North American *N. p. hudsonicus* have been recorded in the Pribilofs (Sladen 1966; UAM unpubl. data).

Limosa lapponica (*baueri*) (Bar-tailed Godwit). Uncommon migrant. Flock of 45 on 26 May 1982, flock of 21 on 3 August 1986, and about 15 in two flocks on 4 August 1986.

Arenaria interpres (*interpres*) (Ruddy Turnstone). Uncommon or fairly common in spring and common in fall; possibly has nested; an adult male on 13 July 1916 (Hanna 1917) was thought to be breeding. Numerous by 22 May 1982; most had moved on by 4 June. Earliest postbreeding, southbound birds on 3 July 1985, 8 July 1966 (D. Eisfeld pers. comm.), 9 July 1983, 11 July 1944 (Beals), 11 July 1982, and 12 July 1986, after which dates species present in flocks of up to 100.

Arenaria melanocephala (Black Turnstone). Casual in spring. Up to five seen 23–29 May 1982. A report without details in August 1954 (Rausch and Rausch 1968) is too vague for evaluation. Known from very few records west of its mainland Alaska breeding range (UAM unpubl. data).

Calidris pusilla (Semipalmated Sandpiper). Casual migrant. Five seen 26 May 1982, one on 3 August 1986, and one (UAM 5259) on 17 August 1985. Casual migrant west and south of its mainland-Alaska breeding range, in Pribilofs (Gabrielson and Lincoln 1959) and Aleutians (Gibson 1981).

Calidris mauri (Western Sandpiper). Uncommon migrant and breeder. One or two seen 30 June to 20 July 1966, behavior indicated nesting (D. Eisfeld pers. comm.). Distraction displays and other behavior pointed to nesting in 1977 (DeGange and Sowls 1978). Present by 22 May (1982) and latest 15 August (1985); small numbers (<5) seen during most summers, whence one specimen (UAM 7340, adult female, 19 July 1997). Seasonal maxima 16 (27 May 1982) and 15 (11 August 1985). Common breeder at St. Lawrence Island (Sauer and Urban 1964, Thompson 1967). St. Matthew Island, Nunivak Island (Swarth 1934), and the Bering coast from the Yukon-Kuskokwim Delta (Gabrielson and Lincoln 1959) to the Alaska Peninsula (Gill et al. 1981) form southern limit of breeding range.

Calidris ruficollis (Red-necked Stint). Uncommon in fall. A few from 3 August (1986) to 17 August (1985), maximum 11 on 17 August 1985. Specimens: UAM 5253, immature female, and UAM 5258, immature male, both 14 August 1985 (PDM and R. Rohleder). Rare migrant on Bering Sea islands (Kessel and Gibson 1978).

Calidris minuta (Little Stint). Casual in fall. Two immatures identified in direct comparison with immature Red-necked Stint 16–18 August 1985; one remained through 21 August (not 1986, cf. Gibson and Kessel 1992). Casual migrant in coastal Alaska from the Aleutians north (ibid.).

Calidris minutilla (Least Sandpiper). Rare breeder. Beals tentatively identified several in 1944, and Klein (1959) reported five during 29 July to 9 August 1957. In 1982 single birds on 27 May and 22 July. A worn adult on 21 July 1986, and an adult with a downy chick the same day. Breeds as far west as the eastern Aleutians (Gabrielson and Lincoln 1959, Murie 1959) and at least occasionally on the Pribilofs (UAM unpubl. data).

Calidris bairdii (Baird's Sandpiper). Rare migrant. Up to six birds 26 May to 7 June 1982. Earliest in fall on 6 August (1986); two on 9 August 1985 and one each on 13 and 15 August 1985. Reported during 2 August to 6 September 1954 (Rausch and Rausch 1968). Nests at St. Lawrence Island (Fay and Cade 1959, Sealy et al. 1971).

Calidris melanotos (Pectoral Sandpiper). Uncommon or fairly common migrant. Recorded 22 May to 2 June 1982, maximum 31 on 24 May. Earliest postbreeding migrants were three on 15 July (1986) and one on 16 July (1985); thereafter in small numbers through observers' late-August departures, maximum 12 on 15 August 1985. Reported during August 1954 (Rausch and Rausch 1968).

Calidris ptilocnemis ptilocnemis (Rock

Sandpiper). Common breeder. "The most abundant bird of the level lands of the islands" in July 1916 (Hanna 1917:409), and still the most numerous breeding shorebird (DeGange and Sowls 1978; KW 1997 pers. obs.). Courtship, territorial defense, and much vocalization by 22 May 1982. Copulation and distraction displays first noted 31 May (1982). Two nests without eggs on 7 June 1982; a nest with full clutch of four on 8 June was subsequently preyed upon by foxes; many nests were later discovered to have been preyed upon. High incidence of nest predation in 1982 might have been influenced by low numbers of voles (*Microtus*). First chicks seen 12 July (1982), one a hatchling, another half-adult-sized. Late nest with two eggs on 21 July (1982), another of four eggs on 15 July (1986), and one nearly fledged downy chick on 24 July (1985). First fledgling seen 17 July 1986. Latest nest date was a hatching on 24 July 1997. These simultaneous, differing stages of the nesting cycle noted as long ago as 1944, when on 21 July Beals noted Rock Sandpipers "gathering in flocks; saw 24 near small lake in one group. Young from downy to flying seen daily. Some nests with eggs being hatched also observed today." One seen in 1982 had been color banded as an adult on the Yukon Delta in 1979.

Calidris alpina (ssp.) (Dunlin). Uncommon or fairly common migrant; possible breeder. Four on 8 July 1940 "acted as if they had nests" (Gabrielson 1944:125). Klein (1959) reported nesting in 1957; no Dunlins seen in summers 1966 (D. Eisfeld pers. comm.) or 1977 (DeGange and Sowls 1978). Twenty on 24 May 1982 and scattered observations during that summer; none in 1983. One adult 21–25 July 1985, 8–10 on 4 August, one on 15 August. None in 1997. Common breeder at St. Lawrence Island (Fay and Cade 1959).

Calidris ferruginea (Curlew Sandpiper). Casual in fall. One juvenile on 14 August 1985. Casual migrant anywhere in the Bering Sea (Kessel and Gibson 1978).

Limnodromus scolopaceus (Long-billed Dowitcher). Uncommon migrant and in summer. Small groups of 4–6 during 22–31 May 1982, maximum 16 on 24 May. Two on 1 July 1982 were only midsummer record. Three adults on 1–2 August (1985) were earliest postbreeding migrants. Species has nested at St. Lawrence Island (Sealy et al. 1971).

Gallinago gallinago (Common Snipe) or *G. delicata* (Wilson's Snipe). Single snipe seen 22 and 24 May and 7 June 1982 were likely either Palearctic *G. gallinago* or Nearctic *G. delicata*. The former is a regular migrant in the western Aleutians (Byrd et al. 1978, Gibson 1981); the latter nests throughout mainland western Alaska (Gabrielson and Lincoln 1959).

Phalaropus lobatus (Red-necked Phalarope). Uncommon breeder. Abundant breeder in July 1916 (Hanna 1917), and Beals reported it so on 10 July 1944 and numerous immatures on ponds on 2 August. Gabrielson (1944) recorded at least 30 on 8 July 1940 and found a nest with four eggs. Klein (1959) recorded it in 1957, and it was probably breeding in summer 1966 (D. Eisfeld pers. comm.). Nested in small numbers in 1977 (DeGange and Sowls 1978). Earliest seen 28 May 1982, and present through July; pairs noted 6 June, copulation 7 June, and a nest with one egg 19 June.

Phalaropus fulicaria (Red Phalarope). Common migrant and in summer; rare breeder. Thousands flew past the ship, heading north, during 8–14 July 1916, "while we were in the ice in the vicinity of St. Matthew"; two flocks in surf on 11 July (Hanna 1917:409). Common at sea and near shore in 1977 (DeGange and Sowls 1978). First seen 25 May (1982), by 31 May in flocks of hundreds, flying about and feeding just offshore. Some still on passage 13 June 1982 (group of 16). Numbers dwindled by end of June; a nest with four eggs on 25 June 1982 is the only breeding evidence. Seen daily in early July 1985, on ocean and along beach, maximum flock of 20+ on 6 July. Postbreeding birds as early as 8 July (1966; D. Eisfeld pers. comm.), after which date numerous.

Stercorarius pomarinus (Pomarine Jaeger). Uncommon migrant and in summer. Eight sightings in July 1977 (DeGange and Sowls 1978). Earliest on 26 May (1982) and 28 May (1983). Except for flock of 21, all sightings of singles or twos. At intervals in summer (one on 27 June 1982, two on 6 July 1985, two or three on 26 July 1986, one on 25 July 1997). Breeding range primarily north of Bering Strait (Gabrielson and Lincoln 1959).

Stercorarius parasiticus (Parasitic Jaeger). Uncommon migrant and in summer. Most frequently observed jaeger in July 1977 (DeGange and Sowls 1978). Earliest on 28 May (1982), maximum four on 10 June 1982; except for two on 26 July 1982 none seen after 1 July (1982). One on 28 June was only report in 1983. In 1985 two on 5 July and singles on 17–19 July and 13 August. Two in August 1957 (Klein 1959). Breeds on Bering coast of Alaska mainland and throughout the Aleutians (Gabrielson and Lincoln 1959), but not on Bering Sea islands.

Stercorarius longicaudus pallescens (Long-tailed Jaeger). Uncommon breeder. On 9 July 1940 a pair seen with two young not able to fly well (Gabrielson 1944). Two nests of two eggs found 8 July 1977 (DeGange and Sowls 1978). Species had arrived by 23 May 1982 and 29 May 1983; maxima in 1982 were five on 2 July and seven on 1 and 7 August. Breeds on Bering coast of Alaska mainland from Seward Peninsula to head of Bristol Bay, and on St. Lawrence and St. Matthew islands (Gabrielson and Lincoln 1959), but not on Alaska Peninsula or Aleutian Islands.

Larus ridibundus (Black-headed Gull). Casual in spring and summer. Recorded 3–8 June 1982, maximum three on 7 June. Adult observed 5 August 1985. Second-year bird on 12 and 18–21 July 1986. Rare in spring and very rare in summer in the Aleutians and Pribilofs (Kessel and Gibson 1978). Breeds as far north and east as the Bering coast of Kamchatka (Lobkov 1986).

Larus canus (ssp.) (Mew Gull). Casual in summer. One identified 7 August 1946 by Gabrielson (Gabrielson and Lincoln 1959); five seen 3 June 1982.

Larus argentatus (*vegae*) (Herring Gull). Rare in summer. Carcass of one molting into third-winter plumage found 4 August 1982. Second-year bird observed 23 July 1985 and a subadult on 4 August. One adult on 11 July 1986. This form breeds in small numbers at St. Lawrence Island (Fay and Cade 1959) and occurs there as a fairly common spring migrant (Thompson 1967).

Larus schistisagus (Slaty-backed Gull). Uncommon throughout year; possible breeder. Adult in colony of Glaucous and Glaucous-winged gulls on 9 July 1966 (D. Eisfeld pers. comm.), and third-year bird seen 26 June 1977 (DeGange and Sowls 1978). An adult and a less-than-adult seen 24 May 1982, and one seen 25 May. One present 26–27 May 1982, and three 2 July. Two noted 29 May 1983. Pair possibly nesting in summer 1982. One seen twice in July 1997. Breeds on Bering coast of Russia as far north as Koryak Highlands (Vaurie 1965); nesting recently recorded near Cape Romanzof, Alaska (McCaffery et al. 1997). Occurs in Bering Sea, Alaska, throughout the year (Kessel and Gibson 1978).

Larus glaucescens (Glaucous-winged Gull). Fairly common throughout year; breeds. Explicitly noted as absent by Hanna (1917). First recorded at St. Matthew during July 1966 by D. Eisfeld (pers. comm.), who noted "several nests in a Glaucous Gull colony on an islet at the northeastern shore." Four adults seen 26 June 1977, and an "immature" seen 13 July (DeGange and Sowls 1978). Almost daily in 1982, usually in flocks with Glaucous Gulls. On 7 July 1982 about 20 of 58 gulls seen were *glaucescens*; fledgling seen with two Glaucous Gull fledglings on 4 August. Breeding of this species among Glaucous Gulls seen in 1982, but not described. Three nests with young found among Glaucous Gulls on 24 June 1983. Breeding observed in 1997 (numbers not recorded) and approximately 50% of all *hyperboreus* and *glaucescens* observations (75–250 daily) identified to species were *glaucescens*. Observed west of St. Matthew Island in February 1970 (McRoy et al. 1971). Nesting reported at St. Lawrence Island in 1913 (Brooks 1915), but Fay and Cade (1959) and Sealy et al. (1971) regarded breeding status there as uncertain. Breeding colonies nearest St. Matthew are at Nunivak Island (Sowls et al. 1978). Northernmost breeding record in Russia is a pair comprising a *glaucescens* and a *schistisagus* that fledged young in 1977 at Geka Bay, at 60° N (near northern Karaginskiy Bay, on the Bering coast of Kamchatka; Kishchinskii 1980).

Larus hyperboreus pallidissimus (Glaucous Gull). Fairly common throughout year; breeds. Recorded nesting in 1916 (Hanna 1917), and a few nesting pairs seen 8 July 1940 (Gabrielson 1944). Population estimated at 2,000 and species regarded as a common breeder along entire coastline in 1977 (DeGange and Sowls 1978). Common breeding

bird in 1982. Pairs on nests as early as 28 May (1983), eggs in nests by 4 June (1983), chicks first seen 24 June (1983), several 1-week-old chicks seen 7 July (1983), one 5- to 7-day-old chick seen 10 July (1982), first flight capable chicks seen 7 August (1983).

Xema sabini (Sabine's Gull). Uncommon in summer. Recorded by Hanna (1917), Gabrielson (1944), Beals (in 1944), DeGange and Sowls (1978), and Goetzmann and Sloan (1982). Seen as early as 1 June (1982) and as late as 12 August (1983 one adult), usually singly or in twos or threes; maximum a flock of five feeding offshore 15 July 1899 (Hanna 1917).

Rissa tridactyla pollicaris (Black-legged Kittiwake). Common breeder. Present in 1916 in colonies of a hundred to a thousand birds (Hanna 1917), and large colonies noted July 1940 (Gabrielson 1944). Populations breeding on cliffs of St. Matthew and Hall islands and Pinnacle Rock estimated in 1977 at 70,000 (DeGange and Sowls 1978). On nesting cliffs by late May (1980s), carrying nesting material 28 May (1982), and sitting on nests with no eggs 2 June 1982. Copulation noted 6 June (1982), first eggs 26 June (1982) and 3 July (1983 one each in six nests). Groups of up to 800 bathed in freshwater lakes almost daily in early summer, groups of only several hundred later in season, and flocks of up to 2,000 observed feeding inshore, often mixed with Red Phalaropes, particularly in early summer. On 26 July 1983, 26 of 55 nests were empty, 24 held one egg, two held two eggs, and three had a single chick; many eggs hatched 26–27 July; one nest held two eggs at least as late as 3 August (1983). Of 31 nests at one colony in 1983, 10 produced eggs, but of those only four hatched, and when last observed on 2 August only one chick was still alive. Beals (in 1944) mentioned having seen no young by 13 August (he departed on 16 August). First chick in 1985 on 1 August probably hatched 31 July.

Rissa brevirostris (Red-legged Kittiwake). Casual or accidental in summer. Adult observed 15 August 1985. Recorded as far north as St. Lawrence Island (Sealy et al. 1971), but does not breed north of the Pribilofs.

Pagophila eburnea (Ivory Gull). Common in winter. On 26–27 March 1968 at ice edge southwest of St. Matthew, Irving et al. (1970: 111) noted "at dusk several flocks of 50 to 100 roosted in rather close groups on larger ice pans apart from the more scattered Glaucous Gulls." Two recorded near St. Matthew 6–7 February 1970 (McRoy et al. 1971).

Sterna hirundo (*longipennis*) (Common Tern). Casual in summer. One observed 2 June 1982, and maximum of four on 6 June 1982. Latest on 27 June 1982. Rare in spring and summer in the Aleutians and Pribilofs, casual as far north as St. Lawrence Island (Kessel and Gibson 1978). Widespread breeder in Kamchatka (Lobkov 1986).

Sterna paradisaea (Arctic Tern). Uncommon migrant and in summer; possible breeder. Recorded July 1899 by A. K. Fisher (Hanna 1917). Two seen in July 1966 in the island interior (D. Eisfeld pers. comm.). One seen 26 June 1977 (DeGange and Sowls 1978). In 1982 first noted on 1 June, maximum 10 on 3 June, last sighting on 26 June; one adult observed 16 August 1985. Breeds at St. Lawrence (Fay and Cade 1959) and Nunivak (Swarth 1934) islands, widely on the adjacent Alaska mainland (Gabrielson and Lincoln 1959), Chukotsk Peninsula (Portenko 1973), Koryak Highlands (Kishchinskii 1980), Kamchatka (Lobkov 1986), and the Aleutians (Murie 1959), but not in the Pribilofs.

Sterna aleutica (Aleutian Tern). Casual in spring and summer. Lone birds on 6 and 20 June 1982, maximum four on 26 June. Breeds locally in Aleutians (Kessel and Gibson 1978) and on Bering coasts of mainland Alaska (ibid.), Kamchatka (Lobkov 1986), and probably Chukotsk Peninsula (Portenko 1973). Pelagic away from colony sites; hardly known at Bering Sea islands (UAM unpubl. data), where it does not nest.

Alle alle (*alle*) (Dovekie). Rare probable breeder. Group of nine seen on the ocean 28 May 1982, and one or two on 12 and 24 June 1983 in auklet colonies. Species recorded 10 July 1985 in auklet colonies (Day et al. 1988). Also probable breeder at St. Lawrence and on islands in Bering Strait (Kessel and Gibson 1978).

Uria aalge inornata (Common Murre) and *Uria lomvia arra* (Thick-billed Murre). Abundant breeders. Both abundant in 1916 (Hanna 1917). Breeding population in 1977 estimated at 600,000, in a ratio of 2.2 Thick-billed to 1 Common murre (DeGange and Sowls 1978).

Beals (in 1944) reported that on 2 August he had still not seen young murres, and that only adults could be seen in nests on 16 August (just prior to his departure); none had hatched in 1977 prior to DeGange and Sowls's (1978) departure on 27 July. First eggs seen 16 July in 1982. Very small *aalge* chick (1–2 days old) seen 31 July (1985), and the first *lomvia* chick seen 2 August (1985). St. Matthew Island is the type locality of *Uria aalge inornata*.

Cepphus grylle (*mandtii*) (Black Guillemot). Uncommon in winter. Small numbers seen in leads in ice off St. Matthew on 7 February 1970 (G. E. Hall pers. comm., McRoy et al. 1971); most numerous bird in 95% ice cover between St. Lawrence and St. Matthew islands in March 1973, usually in ones or twos, maximum a flock of 40 on 4 March (G. J. Divoky pers. comm.). Latest departures in spring included single birds on 1 June 1982 and "most common guillemot in ice" near Hall Island on 8 June 1986 (K. D. Schafer pers. comm.). Because this species winters in Bering Sea pack ice (Kessel and Gibson 1978, Kessel 1989), but Pigeon Guillemot (*Cepphus columba*) retreats south of the ice in winter (Kessel 1989), small numbers of *Cepphus* in March 1968 near St. Matthew were likely this species, rather than *C. columba* as published (Irving et al. 1970).

Cepphus columba (Pigeon Guillemot). Fairly common breeder. Recorded in July 1899 by A. K. Fisher and in July 1916 by Hanna (1917), and described as common during July 1966 (D. Eisfeld pers. comm.). Breeding population estimated at 3,000 in 1977 (DeGange and Sowls 1978). Seen daily in July to August 1982 and 1997.

Synthliboramphus antiquus (Ancient Murrelet). Rare in summer. First seen 1 June 1982, maximum five on 8 June, latest on 24 June. Up to three seen 2–4 June 1983. Four basic plumaged birds seen 8 June 1986 in pack ice off Hall Island and two in alternate plumage 14 June 1986 (K. D. Schafer pers. comm.). Does not breed in the Bering Sea (Sowls et al. 1978), but occurs in summer and fall as far north as St. Lawrence Island (Bédard 1966, Sealy et al. 1971) and the Seward Peninsula (Kessel 1989).

Aethia psittacula (Parakeet Auklet). Common breeder. Hanna (1917) reported great numbers nesting, Gabrielson (1944:271) considered them to be "the most abundant auklet considerably outnumbering the other species in the parts . . . that we explored," and Beals (in 1944) reported them breeding. Population estimated at 18,000 in 1977 (DeGange and Sowls 1978).

Aethia pusilla (Least Auklet). Abundant breeder. Hanna (1917) reported only four flocks and thought that a few might breed. Gabrielson (1944:272) described the species as common on 8–9 July 1940. Population estimated at 175,000 in 1977 (DeGange and Sowls 1978). Chicks first seen 19 July (1982).

[*Aethia pygmaea* (Whiskered Auklet)]. We disagree with Stresemann's (1949) contention (reiterated by Feinstein 1959 and American Ornithologists' Union 1998) that St. Matthew Island should be accepted as the type locality of this species. Gmelin's (1789) tenuous association of his *Alca pygmaea* with Pennant's (1785) "Pygmy Auk" resulted in the concomitant zoogeographic shortcomings of Stresemann's inference. The Kurile, Commander, and Aleutian islands encompass the Whiskered Auklet's range throughout the year (see Vaurie 1965, Byrd and Gibson 1980); in the Bering Sea it is known only from two records of occurrence at St. Lawrence Island and from one in Bristol Bay (Kessel and Gibson 1978). The species does not occur at St. Matthew, and there is no evidence that it ever has occurred there.

Aethia cristatella (Crested Auklet). Abundant breeder. Hanna (1917) reported it rare except for a large colony just south of Glory of Russia Cape. On the other hand, Gabrielson (1944) described it as fairly abundant on 8 July 1940. Breeding population estimated at 110,000 birds in 1977 (DeGange and Sowls 1978).

Cerorhinca monocerata (Rhinoceros Auklet). Casual or accidental in summer. A pair seen 9 July 1986 provides the northernmost report of this species. Breeds on both sides of the North Pacific (American Ornithologists' Union 1998), but, from the Kurile to the Shumagin islands, only locally in the Aleutians (Sowls et al. 1978, Byrd and Day 1986). Two at-sea records between the Aleutians and the Pribilofs (Gould et al. 1982; UAM unpubl. data) provide the only prior reports in the Bering Sea.

Fratercula corniculata (Horned Puffin). Common breeder. Large numbers reported by Hanna (1917). Population estimated to be 10,000 in 1977 (DeGange and Sowls 1978). Present by 22 May 1982, numbers increasing several days thereafter, present on cliffs 29 May; one seen carrying nesting material 18 June 1982. Breeds throughout Bering Sea (Gabrielson and Lincoln 1959).

Fratercula cirrhata (Tufted Puffin). Fairly common breeder. Many nesting colonies mentioned by Hanna (1917). Breeding population estimate to be 3,000 in 1977 (DeGange and Sowls 1978). Present on cliffs 29 May, carrying nesting materials 24 June 1982.

Cuculus canorus (*canorus*) (Common Cuckoo). Casual in summer. A gray morph *Cuculus*, identified as a Common Cuckoo by its white belly with faint ventral barring, was observed well on 16 June 1986 (K. D. Schafer pers. comm.). In spring 1986 migrant Common Cuckoos arrived at the end of May in the Aleutians, where the species was present through late June (UAM unpubl. data).

Nyctea scandiaca (Snowy Owl). Uncommon resident breeder. Albert K. Fisher saw several in July 1899 and found a nest with four young on 14 July (Hanna 1917). Present throughout summer 1944, maximum six (F. L. Beals). One on 7 July 1966 was the only observation that month (D. Eisfeld pers. comm.). One on 3 July 1977 and remains of another found 1 July were the only records during 26 June through 27 July 1977, a season of vole abundance (DeGange and Sowls 1978). One seen at intervals in summer 1982, when vole numbers low. One seen 11 June 1983, and another 19–20 July 1997. Seen on six occasions 7–27 March 1968 from icebreaker in pack ice, one on 22 March ca. 96 km from St. Matthew (Irving et al. 1970).

Asio flammeus (*flammeus*) (Short-eared Owl). Rare in spring and summer. One or two seen 24 May through 6 June 1982, one on 28 June 1983, and one on 31 July 1986. Has nested at St. Lawrence Island (Sealy et al. 1971).

Corvus corax (ssp.) (Common Raven). Rare in summer; probable breeder. Hanna (1917) saw about a dozen in July 1916, and Gabrielson (1944) saw one 8 July 1940. Not reported at all in summer 1944 (F. L. Beals). A few pairs seen from 23 May 1982 on, including two calling and one carrying nesting material at Bull Seal Point on 24 June. One seen 14 June 1986 (K. D. Schafer pers. comm.). Up to three seen 18–25 July 1997. Resident on St. Lawrence Island (Fay and Cade 1959, Johnson 1976), but species unknown at Nunivak (Swarth 1934).

Tachycineta bicolor (Tree Swallow). Casual in spring and summer. Up to three seen 26–28 May 1982 and single birds on 21 and 30 June 1982. Has occurred widely and casually in Bering Sea (see Swarth 1934, Sealy et al. 1971).

Riparia riparia (*riparia*) (Bank Swallow). Casual in summer. One seen 20–21 June 1982. Casual at St. Lawrence Island (Fay and Cade 1959). Breeds annually as far southwest in Alaska as the eastern Aleutians (Kessel and Gibson 1978) and regularly reaches the Pribilofs in spring and summer (UAM unpubl. data).

Petrochelidon pyrrhonota (*pyrrhonota*) (Cliff Swallow). Casual in summer and fall. Single birds seen 28 June 1983 and 3 August 1985. Casual in the Aleutians and on Bering Sea islands (Kessel and Gibson 1978).

Hirundo rustica (ssp.) (Barn Swallow). Casual or accidental in summer. A white-bellied bird (*gutturalis* or *rustica*) seen 14 June 1986 (K. D. Schafer pers. comm.). Old World Barn Swallows are known in the Aleutians and at St. Lawrence Island (Kessel and Gibson 1978).

Delichon urbica (*lagopoda*) (Common House-Martin). Casual or accidental in fall. One seen at close range on 10 August 1983. Previously recorded on Seward Peninsula and Pribilofs (Hall and Cardiff 1978).

Phylloscopus borealis borealis (Arctic Warbler). Casual in summer. Single birds seen 9 July 1940 (Gabrielson 1944) and irregularly during 3–12 July 1985. Longer winged and larger billed than Alaska-breeding *kennicotti*, the only specimen seems to be this subspecies from northeastern Asia (UAM 5248, ad. male, 11 July 1985, B. A. Cooper).

Luscinia calliope (Siberian Rubythroat). Casual in summer. Single males seen 17–18 June 1982 and 9 July 1986. Rare spring migrant in western Aleutians (Gibson 1981), casual in Pribilofs (Kessel and Gibson 1978).

Oenanthe oenanthe (*oenanthe*) (Northern Wheatear). Casual in spring. One seen 24 May through 3 June 1982. Common intercontinen-

tal migrant at St. Lawrence Island and Bering Strait (Kessel and Gibson 1978).

Catharus minimus (*aliciae*) (Gray-cheeked Thrush). Casual in spring and summer. One or two seen 5–15 June 1982. Scarce intercontinental migrant at St. Lawrence Island (Kessel and Gibson 1978).

Turdus obscurus (Eyebrowed Thrush). Casual in spring. One seen 6–7 June 1982. Rare in spring in western Aleutians (Kessel and Gibson 1978, Gibson 1981), casual in spring as far north as St. Lawrence Island (UAM unpubl. data).

Motacilla flava (ssp.) (Yellow Wagtail). Rare or uncommon in spring and fairly common in fall; rare in summer; possible breeder. Hanna (1917) saw a defensive pair on 13 July 1916 that acted as though breeding. Seen 28 May to 23 June 1982, maximum three, and on 24 June 1983. Autumn movement pronounced, earliest on 5 August (1985, 1986), maximum 55+, in flocks of up to 24, on 14 August 1985. Several on 17 August 1985 coincided with observers' departure. Widespread breeding form in Alaska is *M. f. tschutschensis* (Badyaev et al. 1998), but *M. f. simillima*, a regular spring migrant in western Aleutians (Gibson 1981), has nested at St. Lawrence Island (Sealy et al. 1971).

Motacilla alba (*ocularis*) (White Wagtail). Rare in spring and summer. Single birds seen 24 May 1982 through 14 June 1982 and on 2 July 1982. Widespread, rare breeder in coastal western Alaska from Cape Lisburne to Seward Peninsula and St. Lawrence Island; has occurred on mainland as far south as Bristol Bay (Kessel and Gibson 1978).

Motacilla lugens (Black-backed Wagtail). Casual in spring. One seen 2 June 1983. Occurs annually in small numbers in western Aleutian Islands, where has nested, rare spring migrant at St. Lawrence Island, and has bred on the Seward Peninsula (Badyaev et al. 1996).

Anthus hodgsoni (*yunnanensis*) (Olive-backed Pipit). Casual in spring. Seen 3–11 June 1982, maximum 18 on 7 June. Spring 1982 brought large numbers to western Aleutian Islands (UAM unpubl. data). Casual spring migrant from western Aleutians to St. Lawrence Island (Kessel and Gibson 1978).

Anthus cervinus (Red-throated Pipit). Casual in spring. Single birds seen 27 May through 6 June 1982. Rare migrant through western Aleutians (Gibson 1981) and uncommon to fairly common breeder at St. Lawrence Island and in Bering Strait area (Kessel and Gibson 1978).

Seiurus noveboracensis (Northern Waterthrush). Casual or accidental in spring. One seen 6 June 1982. Other far western records include single June birds at St. Lawrence Island (Kessel and Gibson 1978) and on Chukotsk Peninsula (Portenko 1973), and one in August at Nunivak (Swarth 1934).

Passerculus sandwichensis (*anthinus*) (Savannah Sparrow). Casual in spring and summer. Hanna (1917) observed one 10 June 1916 in pack ice south of St. Matthew and another 13 July 1916 at Hall Island. One seen 6 July 1983, and one flew aboard ship just off St. Matthew on 29 August 1988 (J. L. Wells pers. comm.). Extralimital elsewhere west of breeding range in the Pribilofs (Gabrielson and Lincoln 1959), western Aleutians (Gibson 1981), at St. Lawrence Island (Sealy 1967), and on Chukotsk Peninsula (where it has recently nested; Morozov and Tomkovich 1980).

Calcarius lapponicus alascensis (Lapland Longspur). Abundant breeder. Gabrielson (1944) found it fairly common on 8 July 1940, but outnumbered by McKay's Bunting and Rock Sandpiper. Nest with four hatchlings and unhatched egg on 3 July 1985, a fledgling seen 19 July 1985. Fledglings taken or reported 18–25 July 1997, and on 26 July 1986.

Emberiza rustica (*latifascia*) (Rustic Bunting). Casual in spring. Seen 3–11 June 1982, maximum six on 6 June. Rare migrant in western Aleutians (Gibson 1981) and casual at the Pribilofs (UAM unpubl. data) and St. Lawrence Island (Kessel and Gibson 1978).

Plectrophenax nivalis (*nivalis*) (Snow Bunting). Uncommon in spring; possibly breeds. Common on observers' arrival 22 May 1982. Ratio of *nivalis* : *hyperboreus* on 27 May 1982 estimated to be 9:15, on 29 June 1982 14:23; numbers of *nivalis* declined after beginning of June, however. On 24 June 1982 a McKay's Bunting routed a Snow Bunting in a chase and fight. Pair seen 11 June 1982, and on 23 July 1982 a pair acted as if they had a nest nearby but none was found. Not seen in 1983 or in 1997.

Plectrophenax hyperboreus (McKay's Bunting). Common breeder. Discovered to breed

at St. Matthew in 1885 by C. H. Townsend (1887) and observed by all ornithologists in summer since. Arrives as early as "10 or 11 March" (1944, R. V. Anderson *fide* F. L. Beals). From an icebreaker ca. 120 km east of St. Matthew, Irving et al. (1970) saw a few single birds and several small groups in flight toward the island on 20 March 1968.

Pairs and chase flights seen by 29 May (1982); female carrying nesting material 5 June (1983); nest building 18 June (1982); first eggs 23 June (1982); male carrying food to nest 15 June (1983), both parents carrying food to nest 26 June (1983), female carrying food to nest 30 June (1982); and first nestlings 28 June (1983: two 2- to 3-day-old nestlings) and 2 July (1982). Nests on 1 July 1983 had young almost ready to fledge. First fledglings 8–9 July 1940 (Gabrielson 1944), 8 July 1983 (adults feeding fledglings), 9 July 1966 (D. Eisfeld pers. comm.), and 13 July 1985. Several flight capable broods 12 July (1986), many of them 18–25 July 1997. Most nests in rock scree or holes in rock faces; one in mandible of a whale skull; a possible nest in vole-excavated hole. In 1982 nests held 3–5 eggs, commonly four. Flock of 12–15 fledglings 15 August 1985. On 2 July 1982 a female *hyperboreus* and a male *nivalis* were identified together. Winters on Alaska coast of Bering Sea from Seward to Alaska peninsulas (Kessel and Gibson 1978, and citations therein).

Fringilla montifringilla (Brambling). Casual in spring. One or two seen 1–3 June 1982. Annual migrant through western Aleutians (Gibson 1981), casual at Pribilof Islands and St. Lawrence Island (Kessel and Gibson 1978).

Leucosticte tephrocotis umbrina (Gray-crowned Rosy-Finch). Uncommon breeder. Hanna (1917:409) wrote that a few "nest about most of the cliffs but they are much less common than on the Pribilof Islands." No arrival or departure information. Chase flights seen in late May (1980s); pairs seen in early June; carrying nesting materials to cliffs 8 June; male in courtship display 13 June 1982; no nests or young seen in 1982. Begging fledgling seen 26 July 1983. Adults feeding nestlings 14 July 1985; first fledglings that year on 14 August. Winter range not known. Note: a specimen attributed to St. Matthew Island in midwinter (USNM 234,230, male, "22 February 1912") cannot have been collected in any winter month, for it is a black- not yellow-billed bird.

Loxia curvirostra (*minor*) (Red Crossbill). Casual in summer. A female or immature male was seen 5 August 1986. This species and subspecies has a history of casual occurrence on Bering Sea islands (see Thompson and DeLong 1969, Sealy et al. 1971).

Carduelis flammea flammea (Common Redpoll) and *C. hornemanni* (*exilipes*) (Hoary Redpoll). Rare or uncommon in summer; rare breeders. Both recorded, but discussed together because most redpolls not identified to species. Redpolls occur erratically, usually as ones, twos, or small flocks. Hanna (1917) reported a flock of four in July 1916, and Beals saw them at intervals throughout the summer of 1944. Klein (1959) reported over a dozen birds nesting in July and August 1957. Redpolls observed infrequently in May and June 1982; from 21 June almost daily, in flocks of up to 50–60 between late June and late July. Small numbers seen in July 1985, maximum five. A female on 28 June was the only record in 1983. About 10 on 11 July 1986, and a few seen July 1997, including a pair of *C. flammea*, taken in beach driftwood on 22 July, the female in laying condition (UAM 7748, oviduct greatly distended; incubation patch not yet edematous, largest ovum 4 mm).

Carduelis pinus (*pinus*) (Pine Siskin). Casual in spring. Three seen 1–3 June 1982. Far west of breeding range, recorded previously in the Aleutians, Pribilofs, and at St. Lawrence Island (Kessel and Gibson 1978 and citations therein).

Coccothraustes coccothraustes (*japonicus*) (Hawfinch). Casual in spring. One seen 28 May 1982. Casual spring migrant in western and central Aleutian Islands (Kessel and Gibson 1978).

DISCUSSION

One hundred twenty-five species of birds have been recorded at St. Matthew Island. Thirty-one species breed (including annually, occasionally, once, and probably) and another eight are reported as possible breeders. The remaining 86 species occur either as passage migrants or visitants (birds neither migrating nor breeding). These totals are based on sporadic scientific visits to isolated St. Matthew

and Hall islands during the 20th Century, and show that we have yet to determine the complete breeding avifauna, both annual and irregular, and to obtain a full appreciation of the annual variation in abundance (and success) of members of the breeding community. Further, we have only scratched the surface of the subject of the migrations to be observed here. The species composition of this avifauna, and its complexity in movements, breeding, and nonbreeding, reflect the interdigitation of the Old and New world migration systems in this region.

There are a number of obvious changes that have occurred in the fauna of these islands. Among the mammals, polar bears (*Ursus maritimus*) were discussed as common by Townsend (1887) and Elliott (1881; visited in 1874), and have not been noted in summer since. Arctic fox (*Alopex lagopus*) occurs naturally on the islands and undoubtedly has an effect on avian reproductive success. The endemic vole *Microtus abbreviatus* undergoes population cycles (Rausch and Rausch 1968). Reindeer (*Rangifer tarandus*) were introduced in 1944 and later died out (Klein 1968). We think it is unlikely, however, that any of these mammalian factors are related to the long term changes in avian populations observed on this island.

Given the conspicuous absence in 1916 and in the 1940s of the Glaucous-winged Gull, its common presence at St. Matthew since 1966 must be the result of a range expansion into the northcentral Bering Sea. The closely related Glaucous Gull is an ice-adapted arctic species whose southern breeding range limits parallel the extent of winter sea ice. The Glaucous-winged Gull is a North Pacific species that is not ice adapted, and the northern limits of its breeding range can be expected to be determined by the southern extent of ice-locked, but otherwise appropriate, habitat at the beginning of the breeding season as St. Matthew was, for example, when Hanna arrived in 1916 in mid-June. This is precisely one species, therefore, that we would predict to show northward range expansion in the presence of climate change associated with global warming. It is noteworthy then that evidence of this northward range expansion and increase in abundance occur in conjunction with evidence for a northward retreat of the southern limit of summer sea ice in the arctic (Maslanik et al. 1996). St. Matthew is now one of the very few places where Glaucous-winged and Glaucous gulls breed sympatrically in any numbers. We suggest that further increases in mean ambient temperatures in this region might cause a decrease and eventual northward retreat from St. Matthew by the Glaucous Gull. In this regard it is important to note that the Glaucous Gull no longer breeds at its formerly southernmost breeding colony, on Walrus Island in the Pribilofs (Byrd 1997). St. Matthew Island is now the southernmost breeding colony of Glaucous Gulls in the Bering Sea islands.

The eiders present something of a puzzle, because it seems very unlikely that Hanna (1917) confused King and Common eiders. From the evidence, it seems that Common Eiders resumed a former (1899) presence following an absence of unknown duration (1916 at least), becoming a relatively common breeder on the island between 1916 and 1944–1954 and apparently maintaining this status to the present. Hanna's (1917:408) observations of King Eiders ("abundant" and "evidently nesting") is unparalleled elsewhere in the Bering Sea. If King Eiders nested on St. Matthew in 1916, this would represent the historic southernmost edge of the species' breeding range. Today the species is known here in summer only as a rare nonbreeder. There has been a decided change in abundance of the species in summer, and Hanna's (1917) observations of paired birds on fresh water do suggest breeding. This seems to indicate a northward retreat in midsummer abundance, which may represent a northward retreat of the species' breeding range.

Northern Pintails have shown fluctuating numbers, but this seems typical of the species in the region (e.g., see Fay and Cade 1959), and on St. Matthew this may be entirely due to vagaries of the locations of nonbreeding summer individuals. The Semipalmated Plover is a rather conspicuous bird that would have been difficult to miss had it been present as a breeder prior to 1977. It seems to have been present in irregular numbers since. If this is not a recent range extension in the Bering Sea, as seems probable, the species has at least increased in abundance. The Red-necked Phalarope seems to have declined in abun-

dance. Other, less common species may show differences simply due to happenstance. Those listed here, however, suggest genuine differences determined through the reports of a series of competent observers.

The list of species occurring on the island will undoubtedly increase with subsequent visits due to the occurrence of scarce migrants. Regular surveys and monitoring of the breeding species and their population levels might be a simple way to maintain a finger on the pulse of environmental shifts in this region. Because of its central geographic position, St. Matthew Island may represent an important bellwether for monitoring the effects of further global change in the northern Bering Sea.

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MOBBING CALLS OF BLACK-CAPPED CHICKADEES: EFFECTS OF URGENCY ON CALL PRODUCTION

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ABSTRACT.—Many animals advertise the presence of a predator threat through vocal signals. Black-capped Chickadees (*Poecile atricapilla*) use their *chick-a-dee* call as a mobbing call when encountering a perched hawk or owl. This social signal appears to serve as an alert to other chickadees, causing them to rally to the vicinity of the predator and join in a chorus of calling. We asked the question: do chickadees vary the mobbing call in a manner that could convey the immediacy of threat from a potential predator? We examined the responses of chickadees to a taxidermic mount of an avian predator presented at distances of 1 m and 6 m from each subject. Vocal responses were recorded and analyzed for response latency, calling rate, and syllable composition of calls. During 5-min trials, the subjects responded more quickly and produced significantly more *chick-a-dee* calls for predator presentations at the 1-m distance than at the 6-m distance. Alterations of syllable composition of the call also were observed under the two treatments. These results suggest that information about the immediacy of threat or proximity of a predator may be signaled by alteration of the rate of calling, with possible additional information contained in proportional changes in the different syllable types of the call. Studies of referential (symbolic) communication in birds and mammals often have failed to consider the problem of response urgency separately from predator-type labeling in vocal signal design. *Received 14 June 2002, accepted 16 October 2002.*

The antipredator vocal signaling behavior of birds and mammals offers important research opportunities in the functional analysis of animal communication systems. Observations of the utterances of warning calls or mobbing calls in the presence of predators raises questions about the nature of the information content of such vocal signals. If a vocalization contains variations that inform recipients about environmental events, such as the presence of a predator, the signal is referential (Evans 1997). Mammalian studies, especially of primates, call our attention to questions about the cognitive processes involved in signals that employ acoustically distinct, predator-type-specific calls (Seyfarth et al. 1980, Macedonia 1990, Zuberbühler 2000, Manser 2001, Fichtel and Kappeler 2002). The difficulty in obtaining unequivocal evidence for representational cognition in antipredator signaling has led to the notion of "functional reference," which directs efforts toward issues that are possible to address by experimental approaches (Marler et al. 1992, Evans 1997). The concept of functionally referential communication causes one to examine behavioral response to vocal signals, testing the hypothesis that the signals encode information about environmental events, whether a response to the signal is mediated by internal representation or not (Marler et al. 1992).

A problem often arising in the interpretations of predator signaling is the discrimination of predator class labeling from the immediacy of the predation threat. Two different kinds of signals might be used by small birds: one for a raptor circling overhead and a different one for an approaching fox, but these two kinds of predators differ also in the urgency of response required of the prey. Few studies have examined the possible separate effects of predator type and response urgency (Pereira and Macedonia 1991, Manser 2001). Marler et al. (1992) cast the issue in an important light by arguing that antipredator calls usually will contain both motivational (e.g., urgency) information as well as information about kind of predator stimulus, with the relative amounts of the two types of information lying on a continuum.

It was this latter hypothesis that led us to the present study. Well described in the literature is the variable call of the Black-capped Chickadee (*Poecile atricapilla*), the familiar *chick-a-dee* call, from which the species gets its common name. This call is multifunctional, containing information on flock identity, population identity, and location, but it also serves as a predator mobbing call (Ficken et al. 1978, Apel 1985, Smith 1991, Ficken and

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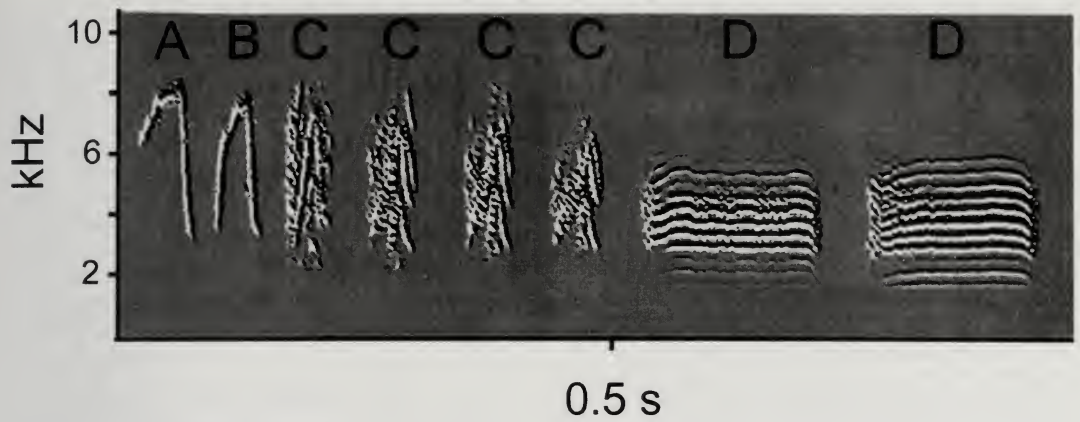

FIG. 1. This *chick-a-dee* call of the Black-capped Chickadee illustrates the four types of syllables (A, B, C, D) usually contained in the call. Each type of syllable can vary in number and this was quantified in calls given by subjects when stimulated by a mount of a Prairie Falcon presented at 1 m and 6 m distances.

Popp 1996, Hurd 1996). During mobbing events, *chick-a-dee* calls are produced as one or more birds approach a predator in a gradual manner, with frequent changes of position, and sometimes attack and dive at the predator, which may induce it to move. Other conspecifics as well as other species are attracted to the site of mobbing. This "harassment" function of mobbing calls has been noted in numerous species of birds (Klump and Shalter 1984, Ficken and Popp 1996).

The *chick-a-dee* call seems well designed for many functions, at least potentially, because the acoustic units that constitute the whole call, the syllables or notes, can combine in various ways numerically to form a very large set of different call types. Although virtually all *chick-a-dee* calls observe the sequential delivery of the four types of syllable in the most complete form of the call (syllable sequence A→B→C→D; Fig. 1), one or more syllable types can be deleted, or produced in differing numbers, indicating a combinatorial signal that has been likened to syntax structures in written language in which letters are recombined to form a variety of different words (Hailman et al. 1985). Therefore, such a variably structured signal as the *chick-a-dee* call encourages one to look for properties of the call that convey different messages. Speculations have been advanced (Hailman et al. 1987) that each of the four kinds of syllables may signal different tendencies for movement. Our study reported here was a first step simply to determine if the *chick-a-dee* call was broadcast with differing rates or the syllable composition altered in response to predator stimulation that differed only in the urgency of the threat, as indicated by a potential predator presented at two different distances from subjects.

METHODS

We obtained Black-capped Chickadees by trapping in natural populations occupying the riparian habitat zone of the Cache La Poudre River (40° 36′ N, 105° 05′ W) near Fort Collins, Colorado, between 4 November 2001 and 7 February 2002. During this period, we brought a few birds at a time into the laboratory, held them for approximately one week during testing, and then released them at the site of capture. At the time of capture, we aged the birds by the distribution of the white band on the outer rectrices (Pyle et al. 1987), which we have found to correlate well with the degree of skull ossification in early and late fall juveniles. We banded the subjects for individual recognition, held them in individual cages (46 cm long, 22 cm wide, 26 cm high) in a common room on natural photoperiod, and fed them sunflower seeds and turkey starter daily.

We conducted stimulus presentations in a large room with the subject in its cage positioned in a sound attenuated box 90 cm above the floor. One side of the box was open and facing a table on which a cardboard barrier prevented the subject from seeing the stimulus located immediately behind the barrier. With a subject on its perch in the cage, the base of the stimulus object was 7 cm above the subject when in view. For the near presentation, we presented the stimulus at a distance of 1 m from a subject's cage, and for the far presentation, the table was moved across the room so the stimulus was 6 m from a subject's cage. A microphone

was located near the subject's cage and recorded all vocalizations.

A trial consisted of transporting (<30 s) the subject in its home cage from the holding room to the test chamber, one of us taking a position out of sight of the subject to later present the stimulus, and the other of us operating the recorder and timing the trial. A trial lasted 5 min. We waited to begin a trial until the subject started to move about in its cage, hopping between perches or eating a sunflower seed, which usually took from 0–4 min. Upon this movement, the tape recorder was activated and one of us pulled a string that slowly moved the stimulus from behind the cardboard barrier into full view of the subject. Beginning when the subject gave its first vocalization we recorded calls for 5 min. Our data thus consisted of 5 min of vocalizations of a subject recorded on one day at one distance to the stimulus and 5 min of vocalizations recorded on the next day at the other distance. We tested half the birds (n = 12) first at the 1 m distance and half (n = 12) first at the 6 m distance.

The predator stimulus was a taxidermic mount of a Prairie Falcon (*Falco mexicanus*) in a natural upright posture as if perched on a branch. Its head was turned toward the cage of the subject so that its face was fully observable. This is a common predator of small birds (Skinner 1938, Bailey and Niedrach 1965) and is seen frequently in the habitats of chickadees in our study area, perched on the buildings and in trees on the campus of the university, and on other commercial buildings in Fort Collins.

We collected an additional data set on eight other chickadees acting as controls for the presentation of the stimulus. We tested these birds at the 1 m distance with the Prairie Falcon and a block of wood of the same size as the predator mount. Four subjects first were presented with the wood block on one day and the predator on the next day, with the reverse order for the other four subjects. This control examined the response of the subjects to a surprising object emerging from behind the cardboard barrier.

From the stimulus sessions, we timed the latency to the first vocalization of each subject, counted the number of calls, and tabulated the constituent syllable types (ABCD) and their numbers in each *chick-a-dee* call. With this matched pairs design in which each subject served as its own control, we examined differences between the two treatments with paired t-tests (Sokal and Rohlf 1981) and an alpha level <0.05 for rejection of the null hypothesis. For comparison of age groups of subjects, we used an unpaired t-test and an alpha level <0.05.

Whereas D syllables are discretely different from other syllable types in the *chick-a-dee* call, and can be assigned accurately to category, the introductory ABC syllables sometimes exhibit intermediates (Hailman et al. 1985, Nowicki and Nelson 1990). When there were intermediates between A and B syllables we applied an arbitrary rule. Intermediates between these two syllable categories were defined as A syllables if the initial upward frequency sweep (Fig. 1) was less than half the length of the downward frequency sweep, or as B syllables if greater than half the range of the subsequent downward frequency sweep. Intermediates between B and C syllables were discriminated by the usually more harsh broadband characteristics of the C syllable (Fig. 1). C syllables that were less noisy had a lower peak frequency than B syllables. There were fewer intermediates between B and C syllables than between A and B. Intermediates were less than 5% of the syllables scored. Our observations of the structure of the syllables of the *chick-a-dee* call followed the comments and classifications used in previous studies (Apel 1985, Hailman et al. 1985, Nowicki and Nelson 1990).

RESULTS

Of the 24 subjects presented with the Prairie Falcon mount at two distances, 15 were >1 year old ("old birds") and 9 were fledged during the breeding season prior to testing ("young birds"). Comparing the two age groups at the same distance from the predator showed that they did not differ significantly either on the latency to the first call or the number of calls given; therefore they were combined for a test of the two distance treatments (Table 1). The subjects responded more quickly to the Prairie Falcon mount when presented at 1-m distance than at 6-m distance, and they also gave more *chick-a-dee* calls to the stimulus presented at 1 m than at 6 m (Table 1). The control tests of the wood block versus the predator indicated a nearly complete absence of response to the wood block (1.4 calls ± 1.0 SE) and a high level of *chick-a-dee* calling to the Prairie Falcon mount (26.3 calls ± 6.4 SE; t = 4.0, df = 7, P = 0.005.

Differences in syllable composition of *chick-a-dee* calls given in the 1-m compared to 6-m treatments primarily were in the relative proportions of A and B syllables. We found that (1) the number of A syllables per call was greater in the 6-m treatment than the 1-m treatment ($\bar{x}$ = 2.45 ± 0.65 SE and 1.53 ± 0.41 SE, respectively; t = 2.43, df = 23, P = 0.029), (2) the number of B syllables was fewer in the 6-m treatment than the 1-m treatment ($\bar{x}$ = 0.83 ± 0.18 SE and 1.45 ± 0.19 SE, respectively; t = 4.28, df = 23, P = 0.001), and (3) the numbers of C and D syllables did not differ significantly between treatments (mean number of C syllables: at 1 m, 0.7 ± 0.4 SE; at 6 m, 0.1 ± 0.5 SE; t = 1.56, df = 23, P = 0.14; mean number of D

TABLE 1. The response of Black-capped Chickadees to presentation of a mount of a Prairie Falcon near (1 m) versus far (6 m) from their cage was significantly greater at the near distance as measured by the latency to the first call uttered (all birds: paired $t = 3.7$, df = 23, $P = 0.001$), and the number of *chick-a-dee* calls given (all birds: paired $t = 2.8$, df = 23, $P = 0.009$). Also, there were no significant differences by these measures when comparing older birds to younger birds at either distance of predator presentation.

	All birds ($n = 24$)		Old ($n = 15$)		Young ($n = 9$)		Old versus young		
Variable	Mean	SE	Mean	SE	Mean	SE	t	df	P
Latency to first call (s)									
Predator near	27.7	13.0	40.7	20.0	6.0	0.8	1.7	22	0.11
Predator far	125.8	28.0	143.0	39.0	86.0	39.0	1.0	22	0.32
Number of calls									
Predator near	24.2	4.9	26.8	7.3	19.9	5.1	0.8	22	0.45
Predator far	13.0	4.5	12.9	5.9	13.9	7.4	0.1	22	0.92

syllables: at 1 m, 2.7 ± 0.4 SE; at 6 m, 2.7 ± 0.5 SE; $t = 0.21$, df = 23, $P = 0.84$; Fig. 2).

Using the total number of syllables in each call as a measure of call length, we found that call length of individuals did not differ significantly when the predator was at a distance of 1 m or 6 m ($\bar{x} = 6.4$ syllables ± 0.3 SE and $\bar{x} = 6.1$ syllables ± 0.5 SE, respectively; $t = 0.54$, df = 23, $P = 0.60$).

DISCUSSION

We conclude that urgency of response in mobbing calls correlates positively with the rate of calling by Black-capped Chickadees, with possible additional information encoded in the syllable pattern of the *chick-a-dee* call. These findings are consistent with the hypothesis that these call features communicate information about the degree of threat posed by a potential predator. From the lack of response to the wood block, it is also evident that the subjects viewed the Prairie Falcon mount as a significant threat, not simply as a surprising object suddenly entering the visual field. Our results are in accord with observations of Apel (1985), who noted that the presentation of a mount of a Sharp-shinned Hawk (*Accipiter striatus*) elicited the highest rate of calling compared to that elicited by mounts of other potential predators. Sharp-shinned Hawks are well known as important predators of small passerine birds. Thus, the high rate of calling to a known significant predator found in Apel's predator presentations to field populations of chickadees, together with our laboratory findings of the highest calling to the near distance presentation of the Prairie Falcon, suggest that the degree of threat is conveyed by high calling rates.

There is some evidence in the literature that chickadees acquire information about the identity of potential predators through a learning process (reviewed in Smith 1991). In the present case, this might lead to the expectation that young chickadees would not respond to the Prairie Falcon mount but older birds would respond strongly. Our results showing that younger birds indeed did respond to the presentations may therefore indicate that by the time of testing they had acquired sufficient experience to recognize the Prairie Falcon as a threat. Given the prevalence of this raptor in the study area, this result may not be surprising.

It has been hypothesized that the different syllables of the *chick-a-dee* call, in the Black-capped Chickadee as well as in the Carolina Chickadee (*Poecile carolinensis*) and Mexican Chickadee (*P. sclateri*), may encode different information (Smith 1972; Hailman et al. 1985, 1987; Ficken et al. 1994; Hailman and Ficken 1996). Substantial data to examine this idea were gathered previously by Apel (1985) in an experimental study of Black-capped Chickadee responses to different kinds of predators, both live and taxidermic mounts, in several contexts. In field presentations during both summer and winter, different types of predators sometimes elicited different combinations of A, B, C, and D syllables (Apel 1985). Apel concluded that the various sylla-

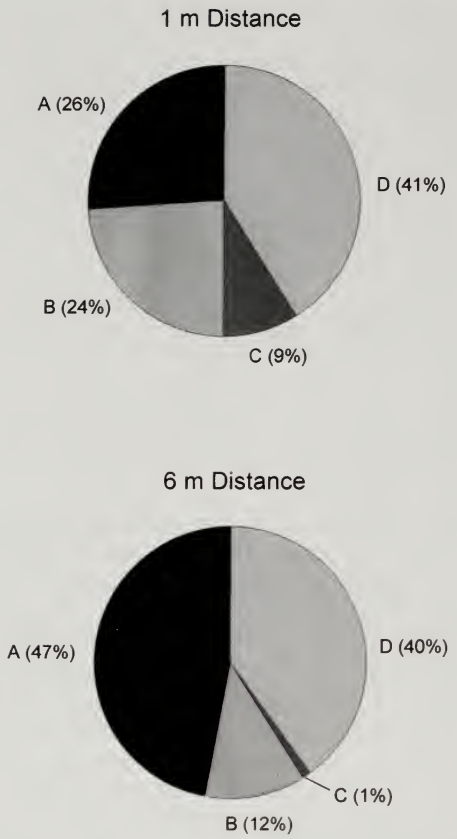

FIG. 2. These pie diagrams illustrate proportional changes in syllable composition of *chick-a-dee* calls given under the two treatment conditions of presentation of a Prairie Falcon mount at a near (1 m) and far (6 m) distance. The data indicate that the chickadees increased the proportion of A syllables and decreased B and C syllables when the predator mount was presented at 6 m compared to 1 m distance. These diagrams summarize the pooled data for all birds, although statistical results (see text) were derived from paired comparisons of each subject's calls under the two treatments.

ble alterations of the *chick-a-dee* call were predator-type dependent and constituted a finely tuned predator recognition response. In particular, Apel hypothesized that an increase in the number of A syllables indicated a higher fear level in subjects, whereas a preponderance of D syllables indicated a less fearful state in the chickadees. In general, the D syllable content of calls was greater in the mobbing context than in nonmobbing situations.

Although we are unable to make conclusions about fear levels in our subjects, the most intense response, as measured by calling rate, was at the 1-m distance to the predator, and this treatment elicited fewer A syllables and more B syllables than the 6-m treatment. Thus, in contrast to Apel's hypothesis, we conclude that a more immediate predation threat causes a chickadee to shift its call to contain fewer A syllables and more B syllables. Apel also noted that on occasions of natural chickadee encounters with raptor predators, strings of A syllables tend to be heard in birds that have retreated to cover and become immobile, perhaps stimulating alertness in others. This observation may suggest an appropriate interpretation for our results of increased A syllables in the 6-m treatment. Seeking cover and becoming immobile could be a good strategy when a predator is first seen at a somewhat distant location. However, we did not monitor activity levels in our subjects under the two treatments of predator distance and therefore have no data with which to address this idea. Although Apel tested subjects with mounts of different kinds of avian and mammalian predators as well as examples of nonpredators of chickadees, an urgency effect was not examined by direct experimentation, e.g., by varying the distance to a given predator, as a possible factor in the chickadee's responses. This large study (Apel 1985), however, set the stage for a more systematic disentanglement of the possible effects of predator type and response urgency on the chickadee mobbing call.

In the Mexican Chickadee, the equivalent *chick-a-dee* call exhibited differences in syllable composition in undisturbed versus disturbed situations in natural populations (Ficken et al. 1994). Two of the syllable types (A, D) predominated in calls on territory with the mate present (undisturbed), but in a mobbing context the AD combination was greatly reduced while C syllables increased (Ficken et al. 1994). Although these results are not easily compared to ours, they suggest that, as in our findings, A syllables are reduced in number under conditions of increased predator threat.

Results of other research on species closely related to Black-capped Chickadees also are instructive. Studies of the antipredator behavior of the Great Tit (*Parus major*) have addressed the question of vocal signaling in response to predators (Curio et al. 1983, Curio

and Regelmann 1985). With restrained live predators at fixed locations as stimuli, Great Tits increased their rate of calling as they approached a predator and decreased the rate as they retreated from the predator. This finding is similar to ours in that calling rate was higher in chickadees for the near presentation of the Prairie Falcon. In other work, a simulated Eurasian Sparrrowhawk (*Accipter nisus*) was presented to captive Willow Tits (*Parus montanus*) at two different apparent distances (10 and 40 m) by use of tiny models (7.2 cm wingspan and 1.8 cm wingspan, respectively) passed over a subject's cage at a height of 2 m (Alatalo and Helle 1990). Only 16% of the birds gave alarm calls to the larger (near) model but 59% gave alarm calls to the smaller (far) model. This simulation of predator distance showed that the propensity to call was low for a more immediate threat, suggesting that calling might increase the risk of predation. No data were provided on the rate of calling or on call structure, so comparisons with our results are limited. However, our subjects all gave mobbing calls at the near distance and did so at a high rate, opposite the general pattern seen in the Willow Tit experiment. A difference of potential significance is that the simulated predator was a moving one in the Willow Tit experiment, whereas the Prairie Falcon, once moved into position, was motionless. This difference could affect the perceived threat of predation.

Alarm call variation in several fossorial mammals appears primarily to be indicative of differing levels of response urgency. Structurally different alarm calls are given by California ground squirrels (*Spermophilus beecheyi*) to approaching aerial and terrestrial predators (Owings and Virginia 1978), but these calls grade into one another and can be given in other contexts (Owings and Leger 1980). These findings led to the interpretation that these variant call structures signal differing degrees of response urgency (Owings and Hennessy 1984). Similar general conclusions have been made for other species of ground squirrels (e.g., Robinson 1981) and marmots (Blumstein and Armitage 1997).

Our results on chickadees parallel these findings in that we view urgency as a descriptor of motivational state, and the differences in calling rate and alteration of syllable composition as reflecting different levels of motivation resulting from differences in the immediacy of predator threat. Therefore, results from studies that find structural differences in alarm calls given to two different classes of predator, such as raptor versus mammal, sometimes could be misinterpreted as representing more complex cognition than is warranted, unless the immediacy of the threat is examined experimentally as a possible cause of the observed differences in alarm calls.

The systematic teasing apart of predator labeling and response urgency as causes of differences in vocal signals seldom has been accomplished, in spite of the simple experimental design required: at least two predator classes each presented at two levels of response urgency. Lemurs, for example, make their call selection appropriate to the predator class with only minor vocal alteration signaling urgency in avian predation simulations (Macedonia 1990, Pereira and Macedonia 1991). Other studies also have found predator class labeling independent of urgency (Seyfarth et al. 1980, Fichtel and Kappeler 2002). In social mongooses (*Suricata suricatta*), apparently both predator type and urgency information are contained in their antipredator calls (Manser 2001).

Our results on chickadee mobbing calls suggest that calling rate and some structural alterations vary with the immediacy of predator threat. Whether these variations in call properties represent signals that effect different behavior patterns in conspecifics in the area of the calling bird is unknown. Our results call attention to the need for studies of the responses of receivers to determine if, for example, the intensity of mobbing behavior or defensive escape and hiding are elicited by the call variations.

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Short Communications

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Nest, Egg, and Nesting Biology of the Snowy Cotinga (*Carpodectes nitidus*)

César Sánchez-M.[1]

ABSTRACT.—I describe the nest, egg, and nesting behavior of the Snowy Cotinga (*Carpodectes nitidus*) in La Selva Biological Station, Costa Rica. The nest was placed 7.5 m high on a fork formed by four branches of a leafless tree. The nest was a simple platform made of dry tendrils and lichens. It contained a single large egg, which took at least 27 days to hatch. The nest and chick were predated the day after hatching. Both nest and egg characteristics resemble those of other cotinga species. *Received 29 January 2002, accepted 22 August 2002.*

Although Neotropical cotingas are conspicuous, their breeding behavior is very poorly known. The genus *Carpodectes* is no exception (Snow 1982). The Snowy Cotinga (*Carpodectes nitidus*) is a canopy dweller inhabiting wet forest on the Caribbean lowlands of Central America, from northern Honduras to Panama (Ridgely and Gwynne 1989, Stiles and Skutch 1989). In Costa Rica, the Snowy Cotinga is considered common to rare along its geographical range, which extends from the northeastern slope of the Guanacaste mountain range to the Panama border. The scarce information concerning its nesting was obtained in March 1891, when C. F. Underwood collected a nestling from its nest in Costa Rica (Snow 1982). Another nest was found, also in Costa Rica, in April 1999 (Klebauskas and Pacheco 2000). This nest was a small cup placed in a three-pronged fork, 10–12 m up in a leafless tree. It contained at least one nestling. Here I describe the nest and the first known egg of the Snowy Cotinga, with some information on its nesting behavior, recorded from 21 April to 4 May 2001.

The nest was found by R. G. Campos at La Selva Biological Station (10° 26′ N, 84° 00′ W, 65 m elevation), in Sarapiquí, Heredia, Costa Rica. The nest was placed at the junction of four branches on a sandbox tree (*Hura crepitans*, Euphorbiacae) at 7.5 m above the ground. The sandbox tree is a deciduous, shade intolerant species, inhabiting tropical dry and tropical moist life zones (Hartshorn 1983). The tree was about 11 m tall with a 25-cm dbh. When the nest was built and the egg laid (late March to early April), it was completely leafless. The nest with a single egg was discovered on 7 April 2001. The area around the nest was dominated by young second growth, including pastures and scattered medium-sized trees (10–20 m): *Cecropia* spp., *Spondias mombin*, palms, and a few tall trees. The tree containing the nest was very exposed, since it was one of the tallest and it was only 10 m away from the main entrance road to the station. I first checked the nest on 21 April 2001; by then the tree had small young leaves and leaf buds. I made the observations from a ladder placed on top of a van; I was about 4 m high and 10 m from the nest.

The nest was a small cup, which barely allowed the female space upon which to sit (Fig. 1). The nest was made of small dry twigs and dry woody tendrils with some lichens. Its structure was simple, and the few materials used seemed loose, apparently held together by the branches upon which it was placed. I estimated the size of the nest and egg in relation to the female's body, using pictures taken from the nesting tree and a female specimen collected at the same location (UCR # 1567). The nest was about 7–10 cm wide at its maximum diameter and 3 cm in height. Although it was not possible to estimate the depth of the inner cup, it was shallow enough to allow observation of the egg from ground level.

I estimated the egg to be about 25.4 mm long, and about 20 mm wide (Fig. 2). Because only half of the egg was seen, it was not possible to make an accurate estimate of its width. It was possible, however, to see that its shape was oval. The color was a very light greyish-white, with

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FIG. 1. Female Snowy Cotinga (*Carpodectes nitidus*) at the nest, La Selva Biological Station, Costa Rica, 27 April 2001. Photograph by M. Saborío.

light brown blotches concentrated at the blunt end of the egg (wreathed).

I observed the nest on 25, 27, and 28 April 2001, while the female was incubating. During 17 hours of observation, she left the nest seven times; the mean length of her periods off the nest was 32.5 min ± 8.8 SD, 19% of the observation time. Four of these exits occurred between 8:53 and 10:00 CST. While on the nest, the female changed position frequently, rolling the egg a mean of every 7.1 min ± 4.3 SD (n = 22). Usually during the hottest part of the day, the female stood on the nest shading the egg (without making contact with it), positioning her back to the sun. I did not observe any interaction with other individuals of the same or other species that flew into or near the nest tree. I observed male Snowy Cotingas within about 25 m of the nesting tree, but none of them approached the nest and I did not hear any vocalizations during the observation period.

The chick hatched on 3 May 2001 (J. Alvarado pers. comm.). The following day the nest and nestling had disappeared, probably predated. The egg took at least 27 days to hatch, a relatively long time for a passerine of this size, although similar to the incubation periods of other cotingas (Snow 1982).

The characteristics of the nest were similar to those of some other cotingas (e.g., white-winged cotingas, *Xipholena* spp.) and pihas

FIG. 2. Nest and egg of the Snowy Cotinga (*Carpodectes nitidus*), La Selva Biological Station, Costa Rica, 27 April 2001. Photograph by M. Saborío.

(*Lipaugus* spp.; Skutch 1969, Sick 1993). Similarities in nest shape and material, as well as egg shape and color patterns, between the Snowy Cotinga and Pompadour Cotinga (*X. punicea*), support the hypothesis that *Xipholena* is most closely related to *Carpodectes*, as suggested by Snow (1982).

The observations herein and the nest description of Klebauskas and Pacheco (2000) suggest that the Snowy Cotinga may prefer to nest in leafless trees located in semi-open habitats. Snow (1976) suggested that nests built in trees outside the forest, and isolated from other trees, may be less vulnerable to predation than those within the closed forest. These observations seem contrary to the general rule that nests of most cotingas are highly inconspicuous (Snow 1982).

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Black Oystercatcher Natal Philopatry in the Queen Charlotte Islands, British Columbia

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ABSTRACT.—Very little demographic data is available for rocky intertidal shorebirds, including the long-lived Black Oystercatcher (*Haematopus bachmani*). In this paper we report on Black Oystercatcher chick production from 1992 to 2000, age of first breeding and natal philopatry in Laskeek Bay, Queen Charlotte Islands, British Columbia. Five percent of birds banded as half-grown chicks returned to breed in the same area. Known-age birds were 5 years old when first found breeding. This constitutes the first published evidence of natal philopatry for this species. *Received 4 January 2002, accepted 5 August 2002.*

Black Oystercatchers (*Haematopus bachmani*), resident rocky intertidal shorebirds found throughout the Pacific Coast of North America, are considered a species of serious conservation concern in Canada (Donaldson et al. 2000). Previous studies have examined the foraging ecology, breeding biology, and habitat requirements of the Black Oystercatcher throughout its range (see summary in Andres and Falxa 1995). However, most research has been too brief to collect demographic information on this long-lived species. Demographic information, such as dispersal or natal philopatry, is of key importance to understanding population dynamics (Hanski 2001).

In 1992, the Laskeek Bay Conservation Society initiated a long term monitoring program based on marking and subsequent resightings of Black Oystercatcher young in Laskeek Bay, Queen Charlotte Islands. In this paper, we report on Black Oystercatcher chick production, age of first breeding and natal philopatry in Laskeek Bay from 1992 to 2000.

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METHODS

Laskeek Bay is situated on the east coast of Moresby Island, in the Queen Charlotte Islands archipelago, British Columbia (52°54′ N, 131°36′ W). The Laskeek Bay Conservation Society began observations of Black Oystercatcher breeding biology and banding of oystercatcher young on islands and islets in Laskeek Bay in 1992, and has conducted this work annually since then.

We surveyed all known Black Oystercatcher breeding sites and searched all islands and islets in Laskeek Bay for new breeding pairs between 20 and 30 May of each year. We used binoculars or a spotting scope to check all birds for the presence or absence of leg bands. We revisited identified breeding territories between 1 and 5 June to determine the status of the breeding attempt (eggs and/or young chicks present). One island, Kingsway Rock, was not visited during 1992, 1993, or 1995 (although it was visited in July to search for young to band), so only surveys from 1996 onward represent complete censuses of the number of breeding pairs and marked birds in the study area.

During early July, we revisited all breeding sites that had been active in June. We banded chicks >100 g with a band scheme unique for each year. Depending upon the year, we marked chicks with combinations of color darvic plastic wrap-around bands or a single alpha-numerically engraved plastic band. Because the engraved layer of the wrap-around leg bands did not remain intact, those bands appeared black (the inner layer) when resighted during later years (see Hazlitt 2001).

RESULTS AND DISCUSSION

We located 16–35 active Black Oystercatcher territories (sites where clutches were found) each year (Table 1). We located breeding territories on nine islands or island groups, each with 1–9 breeding pairs in a given year. A mean of 29 Black Oystercatcher pairs bred in the Laskeek Bay area each year from 1996–2000 (the period with complete surveys). The number of active pairs or clutches located each year varied, likely a result of variation in timing of the initial survey. Poor weather conditions often delayed the May survey, so observers may have missed active pairs or first-laid clutches depredated early in the season.

TABLE 1. Number of clutches observed and chicks banded for Black Oystercatchers breeding in the Queen Charlotte Islands, British Columbia. Mean annual numbers of occupied breeding territories discovered are in parentheses.

Variable	Location	Year									All years
		1992	1993	1994	1995	1996	1997	1998	1999	2000	
Clutches	All locations	16	28	28	34	33	16	35	35	24	249
Chicks	East Limestone (3)	2	5	5	4	0	0	0	2	3	21
	Reef Island (7)	7	4	4	6	3	3	1	4	0	32
	South Low Island (5)	4	7	0	3	6	0	0	0	0	20
	Kingsway Rock (2)	0	0	1	2	0	3	0	0	6	12
	Lost Islands (6)	0	0	0	0	0	0	0	3	0	3
	Skedans Islands (6)	0	3	3	3	3	0	0	0	5	17
	Low Island (2)	0	4	1	4	0	0	2	1	2	14
	Total chicks banded	13	23	14	22	12	6	3	10	16	119

The maximum number of active breeding pairs in the Laskeek Bay area was 35 pairs. We marked 119 Black Oystercatcher chicks between 1992 and 2000, with a minimum of three chicks banded during 1998 and a maximum of 23 chicks during 1993 (Table 1).

During the summer of 1995, we sighted three nonbreeders banded as nestlings the previous year: two on East Limestone Island and one on the Skedans Islands. We also observed three more banded nonbreeders during 1997; one bird had been marked in 1994 and two others during 1995 or 1996.

During the census of breeding pairs during May and June of 1999 and 2000, we observed three and four, respectively, banded oystercatchers holding breeding territories. The marked breeding birds at South Low Island and the Skedans Islands were observed during both years and had been marked as chicks in 1994. Black Oystercatchers show strong philopatry to breeding territories (Andres and Falxa 1995, Hazlitt and Butler 2001), so we assume the banded birds observed on these territories during both years were the same individuals. The marked adult observed breeding on South Low Island was trapped while incubating in 2000 and was identified as a chick that had been banded on Kingsway Rock 7 km away. The remaining two marked birds bred on Kingsway Rock and the Lost Islands. These birds had been marked in 1995 or later. Both birds of known age were first observed breeding at 5 years. The bird sighted at the Lost Islands was ≤4 years at first breeding, while the other banded bird observed was ≤5 years at age of first breeding.

Although we banded 119 young during the study, relatively few marked birds were resighted. We sighted a maximum of only six marked nonbreeding birds, all within three years after banding. Our unequal banding effort likely influenced the probability of resighting individuals; however, most marked chicks disappeared during a similar study in southern British Columbia where banding effort was consistent (Hazlitt and Butler 2001).

We discovered four known-age breeders holding breeding territories by 2000. We observed that Black Oystercatchers in Laskeek Bay began breeding at 4–5 years of age. This finding is supported by independent observations for this and other oystercatcher species, and probably is characteristic of the genus (Harris 1967, Nol and Humphrey 1994, Andres and Falxa 1995). If we assume that no birds bred before 4 years old, then the observed local recruitment rate was 4/84 = 5% (84 chicks were banded before 1997). It is likely that many marked fledglings perished during the first winter, a pattern documented by Kersten and Brenninkmeijer (1995), who demonstrated a high mortality rate (60%) for hatch-year Eurasian Oystercatchers (*Haematopus ostralegus*). Although highly variable between years, juvenile mortality in the Eurasian species can be particularly low (10%) during years with extreme winter weather conditions. Some Black Oystercatcher chicks may have dispersed from their natal sites; however, we suggest that most perished.

Although natal philopatry has been documented in the Eurasian Oystercatcher (Harris 1967, Heppleston 1972, Kersten and Bren-

ninkmeijer 1995), there are no published records of individual American Oystercatchers (*H. palliatus*; Nol and Humphrey 1994) or previous records of individual Black Oystercatchers (Andres and Falxa 1995) breeding at natal sites. The long term nature of this project has provided the first records of age of first breeding and the first published evidence of natal philopatry for this species.

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Ring-Necked Pheasant Parasitism of Lesser Prairie-Chicken Nests in Kansas

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ABSTRACT.—We report observations of Ring-necked Pheasants (*Phasianus colchicus*) parasitizing Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) nests in native sand sagebrush (*Artemisia filifolia*) rangeland in southwestern Kansas. We found low incidence of interspecific nest parasitism as only 3 of 75 prairie-chicken nests were parasitized. Two of the three parasitized clutches hatched, but no Ring-necked Pheasant chicks were known to have survived. *Received 12 March 2002, accepted 30 August 2002.*

The distributions of the Ring-necked Pheasant (*Phasianus colchicus*) and the Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) overlap in Kansas (Thompson and Ely 1989). Ring-necked Pheasants (hereafter pheasants) are believed to compete for resources and disrupt the behavior of other galliform birds (Sharp 1957, Vance and Westemeier 1979, Kimmel 1988, Westerskov 1990), particularly

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the Greater Prairie-Chicken (*T. cupido*; Westemeier et al. 1998). Interactions include disruption of courtship and mating behavior, displacement of birds from traditional breeding grounds, competition for food, and nest parasitism (McAtee 1945, Sharp 1957, Vance and Westemeier 1979). We are not aware of any previously published reports of pheasants laying eggs in nests of Lesser Prairie-Chickens. We report three such observations and the fates of young pheasants and prairie-chickens in the resulting mixed broods.

We monitored nesting activities of radio-marked prairie-chicken and pheasant hens in native sand sagebrush (*Artemisia filifolia*) habitat in Finney County, Kansas (37° 52′ N, 100° 59′ W) to investigate possible negative interspecific interactions during nesting, brooding, and rearing periods from April to August, 1997–1999. We radio marked 84 Lesser Prairie-Chicken hens; 64 of these were tracked to at least one nest, 11 left the study area, 4 died prior to nesting, 5 were not known to have nested, and 11 renested after failure of the first nest. We also radio marked 22 pheasant hens within sagebrush rangelands and in adjacent croplands during 1997 and 1998, of which 14 nested once, 4 died, 4 had transmitters fail prior to nesting, 7 renested after failure of the first nest, and 1 initiated a third nest after two failed attempts.

We inspected nests near the onset of incubation and again after hatching or nest failure. We estimated nest success as the proportion of nests hatching ≥1 egg, and hatching success as the number of eggs hatched divided by initial clutch size (Westemeier et al. 1998). We determined the occurrence of interspecific nest parasitism from the appearance of eggs within a clutch. Generally, the size and coloration of these two species' eggs were distinctive enough to differentiate them in the field. Lesser Prairie-Chicken eggs were pale yellow to ivory, and in some instances had fine speckling; pheasant eggs were glossy olive-brown to blue-gray without speckling (Baicich and Harrison 1997). We were unable to ascertain parasitism rates from egg-laying intervals (Yom-Tov 1980) because nests were visited infrequently. We flushed Lesser Prairie-Chicken broods at 10-day intervals to monitor survival of both Lesser Prairie-Chicken and pheasant chicks in mixed species broods (Jamison 2000).

Nest success was 8% (n = 25), 42% (n = 19), and 32% (n = 31) during 1997–1999. Three (4%) of 75 Lesser Prairie-Chicken nests were parasitized by pheasants. We did not attempt to determine whether intraspecific parasitism occurred in pheasant nests, but we did not observe obvious egg dumping. Clutch sizes of the radio-marked pheasant hens (mean = 10.9, SE = 0.54, range = 8–17 eggs) was similar to the mean of 11 eggs previously reported for the species (Johnsgard 1999, Giudice and Ratti 2001).

All instances of interspecific parasitism occurred during 1998. Two of the three parasitized clutches hatched while only 18 of 72 (25%) unparasitized clutches hatched. Hatching success of parasitized and unparasitized nests was 70% and 72.5%, respectively. Based on estimated nest initiation dates and clutch sizes of Lesser Prairie-Chicken nests, we assumed the parasitized nests were the first nesting attempts of the host species. The ratio of Lesser Prairie-Chicken : Pheasant eggs in the three parasitized nests were 15:3, 10:2, and 8:1. The clutch of 8:1 eggs was depredated a few days after incubation began. The clutches of 15:3 and 10:2 eggs hatched 9:2 and 8:1 eggs, respectively. Three prairie-chickens from the mixed brood of 11 chicks survived to ≥60 days after hatching, but no pheasants were known to have survived >9 days after hatching. The mixed brood of nine chicks suffered total loss ≤14 days after hatching.

DISCUSSION

We believe the parasitism rate in our sample of 75 nests likely reflects current parasitism rates in similar habitats of southwestern Kansas. While speculative, this conclusion is supported by the absence of obvious intraspecific parasitism by pheasants. Pheasant parasitism rates (mean = 15%, range = 3–43%) on Greater Prairie-Chicken nests in Illinois were negatively correlated with egg hatching success; 85% and 63% of eggs in unparasitized and parasitized nests hatched, respectively (Westemeier et al. 1998). Apparent nest success was similar between parasitized (51%) and unparasitized (43%) nests (Westemeier et al. 1998). We were unable to assess

relationships for hatching or nest success due to the low rate of parasitism in our study.

The greatest potential for negative effects from nest parasitism occurs in the nest because of the differential incubation periods (26 days for Lesser Prairie-Chickens, 23 days for pheasants; Giesen 1998, Giudice and Ratti 2001). Partial or complete nest abandonment may occur when the brood parasite's eggs hatch prior to the host's eggs. Thus, in areas with high pheasant densities (e.g., Illinois) and limited nesting habitat, nest parasitism may negatively affect demographic rates.

Although fragmented, currently available habitat in southwestern Kansas may be extensive enough that these species can coexist with little competition for nest sites. Lesser Prairie-Chickens and pheasants occupy different niches in southwestern Kansas, large tracts of native prairie versus fragmented prairie or old fields juxtaposed to extensive agriculture, respectively (CAH unpubl. data). Bennett (1947) reported that pheasant densities were positively correlated with rates of intraspecific nest parasitism in Iowa. As nest site availability decreased (e.g., in Iowa and Illinois), rates of inter- and intraspecific nest parasitism increased (Bennett 1947, Westemeier et al. 1998). Thus, nest parasitism by pheasants appears to be density dependent. If true, further fragmentation of native habitat in southwestern Kansas may increase parasitism rates. Furthermore, our limited observations indicate that pheasant chicks may not survive well with interspecific brood hens, and we are not aware of any published reports of chick survival in wild mixed broods.

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Turquoise-browed Motmot (*Eumomota superciliosa*) Feeds by Artificial Light

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ABSTRACT.—We report the Turquoise-browed Motmot (*Eumomota superciliosa*) feeding in the evening on insects attracted to artificial lights. This behavior has been observed in few diurnal bird species, and has not been reported previously for the family Momotidae. Although more than one motmot engaged in this behavior at one site in El Salvador, and feeding success appeared favorable, we have not observed the behavior at other sites in El Salvador, suggesting that the behavior has not spread through the population. *Received 14 June 2002, accepted 20 November 2002.*

Despite a tremendous increase in artificial lighting at night during the last century, remarkably few bird species appear to have adapted to the rich insectivorous food sources that congregate around these lights. Individual birds that learn to feed at such lights during the night might gain fitness benefits. Any cases of individual birds using this potential feeding source could signal the beginning of an evolutionary trend.

Instances of feeding by diurnal birds around artificial light sources at night have been reported for species in the orders Falconiformes (Tryjanowski and Lorek 1998), Gruiformes (Hopkin 1985), Charadriiformes (Blackett 1970), Apodiformes (Goertz et al. 1980, Freeman 1981, Sick and Texeira 1981), and Passeriformes (King 1967, Felton 1969, Blackett 1970, King and King 1974, Bakken and Bakken 1977, Sick and Texeira 1981, Speich 1982, Frey 1993, and Bulgarini and Visentin 1997). Most of these observations were from the West Palearctic region. Here we report an instance of nocturnal feeding by the Turquoise-browed Motmot (*Eumomota superciliosa*), a diurnal Neotropical species in the family Momotidae (Coraciiformes). No species in this family previously has been reported to feed nocturnally on insects attracted to artificial lights (Snow 2001). The Turquoise-browed Motmot, although active diurnally, also is crepuscular, as we have heard them vocalizing before dawn and watched them hunt so late in the evening that they could be identified only by silhouette.

During 1975 and 1976, WAT observed Turquoise-browed Motmots hunting by the lights of electric lamps. At Las Minas de San Cristobal, Morazán Dept., El Salvador (13° 35′ N, 88° 05′ W; elevation 200 m), an unshaded 100-watt lamp had been suspended from a mango tree (*Mango indica*) to illuminate a residential yard. About 30 m away, a dim street lamp illuminated the entrance to this yard. Turquoise-browed Motmots came regularly to feed on insects attracted by the lamps (M. Airey pers. comm.). WAT verified these observations during the evenings of 14 May 1975 and 7 May 1976, when a single motmot arrived at the mango tree at 19:02 (CST) and departed at 19:35 the first evening, and arrived at 19:07 and departed at 19:46 the second evening. Those arrival times were 42 min and 52 min after sunset. Times of arrival and departure of the bird under the street lamp were about the same, but precise times were not recorded. The birds never returned later during the night, according to our limited observations and those of M. Airey, which were made until midnight.

A comparison of the nocturnal feeding behavior of the motmot in the mango tree with diurnal feeding suggests that nocturnal feeding may be more efficient. The night-feeding motmot sallied 15 times after flying insects during a 10-min period, 5 times with obvious success, and dropped once to the ground to seize a fluttering insect. Large prey were carried back to a

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perch and rapped against it sharply ≤8 times to prepare it for eating. If a large insect was dropped to the ground and lay quiet, it was ignored. In daylight we rarely have seen motmots sally for flying prey, although Skutch (1947) and Orejuela (1980) reported that it was not unusual. The species takes much of its prey by dropping suddenly to the ground or to low foliage from perches ≤30 m away (WAT and OK pers. obs.). The frequency of foraging attempts is relatively low (we do not have quantitative data, but suspect that the mean rate of forays is <5 per 10 min).

A single session at the artificial lamps seemed to satisfy the immediate needs of a motmot, as it would not be seen again that evening. Artificial lights and Turquoise-browed Motmots are both abundant throughout parts of El Salvador and neighboring countries, yet we have not observed nor heard of other cases of motmots learning to feed near lights during nearly 20 years of observing birds across El Salvador.

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Fan-tailed Warbler Foraging with Nine-banded Armadillos

Oliver Komar[1,3] and Cullen K. Hanks[2]

ABSTRACT.—We report Fan-tailed Warblers (*Euthlypis lachrymosa*) foraging in association with the nine-banded armadillo (*Dasypus novemcinctus*) in El Imposible National Park, El Salvador. Although the warbler is known to forage opportunistically at ant swarms, this is the first report of commensal feeding with a mammal. *Received 5 April 2002, accepted 21 September 2002.*

Commensal foraging strategies have evolved in numerous species of birds (Willis and Oniki 1978, Dean and MacDonald 1981, Roberts et al. 2000). Birds forage on prey flushed by a wide variety of animals, including ants (Willis and Oniki 1978, Roberts et al.

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2000), other birds (Baker 1980, Robbins 1981), maned wolves (*Chrysocyon brachyurus*; Silveira et al. 1997), primates (Stott 1947, Boinski and Scott 1988), cetaceans (Evans 1987), ungulates (Heatwole 1965, Dean and MacDonald 1981, Källander 1993), and humans (Skutch 1969).

Armadillos (Mammalia: Dasipodidae) disturb invertebrates by digging in and overturning leaf litter. However, we found only one report of a bird foraging in association with an armadillo; an Ovenbird (*Seiurus aurocapillus*) was observed in Florida apparently gleaning insects flushed by a nine-banded armadillo (*Dasypus novemcinctus*; Levey 1999). The Fan-tailed Warbler (*Euthlypis lachrymosa*) also is an insectivorous ground-feeding warbler (Passeriformes: Parulidae). Fan-tailed Warblers are opportunistic foragers known to follow army ant swarms (Sutton 1951; OK and CKH pers. obs.) and occasionally other birds (Robbins 1981). Here we document, for the first time, observations of Fan-tailed Warblers foraging in association with a mammal, the nine-banded armadillo.

We observed armadillos and Fan-tailed Warblers opportunistically during 23 days of field work at Parque Nacional El Imposible. This park is a 5,000-ha tropical forest (mixed semideciduous and evergreen) in southwestern El Salvador (13° 51′ N, 89° 59′ W). We worked in the park during December 2001, and January and February 2002. This period corresponds to the dry season.

On two occasions we observed single Fan-tailed Warblers foraging alongside single nine-banded armadillos. Each observation lasted 10 min while the animals were ≤10 m from the observer. In both cases, the warblers actively foraged <1 m from the armadillos, occasionally hopping or landing within 10 cm. The armadillos moved slowly through the forest, foraging noisily in the leaf litter. As the armadillos foraged, the warblers fanned their tails and sallied from low perches as they typically do when chasing insects. We were unable to confirm any captures. We did not detect any response by the armadillos toward the birds.

We interviewed two park guards who had observed this foraging association previously. Over 15 years, V. Campos (pers. comm.) recalled seeing Fan-tailed Warblers foraging in close proximity to individual armadillos on four occasions, twice involving two warblers, once involving three warblers, and once involving four warblers.

Fan-tailed Warblers occasionally approached humans at our study site (OK pers. obs.). This odd behavior may be explained as part of a foraging strategy that includes following mammals, and suggests that the species may take advantage of a wide variety of disturbances in the leaf litter that provide foraging opportunities, whether caused by army ants, other birds, or mammals. Further research should investigate whether commensal foraging leads to increased fitness in the Fan-tailed Warbler.

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Twine Causes Significant Mortality in Nestling Ospreys

Charles R. Blem,[1,3] Leann B. Blem,[1] and Peter J. Harmata[2]

ABSTRACT.—Ospreys (*Pandion haliaetus*) over much of Montana incorporate large amounts of bailing twine in their nests and active nestlings sometimes become entangled and perish. We observed 12 occurrences of entanglement in 260 nests during three years of study. Disposing of the twine or cutting the twine into smaller pieces when removing it from hay bales could reduce or eliminate the problem. *Received 17 June 2002, accepted 4 December 2002.*

Causes of mortality for young Ospreys (*Pandion haliaetus*) include natural events such as starvation, predation, lightning, wind storms, and various accidents (Bent 1937, Leenhouts 1987, Poole 1989, Johnsgard 1990). Death occasionally occurs because of human activities (e.g., pollutants, electrocution on power lines, collision with man-made structures; Schmidt 1973, Munoz 1990). This paper documents an uncommon but important cause of death for ospreys over a wide area in Montana and presents a simple suggestion to reduce its impact.

During surveys of osprey nests in Broadwater and Lewis and Clark counties, Montana (47° 11′ N, 112° 37′ W; 1998 and 1999, 156 nests; PJH), and the Flathead Lake catchment basin, Lake and Flathead counties, Montana (48° 53′ N, 114° 02′ W; 2001, 104 nests; CRB and LBB), we visited each nest several times during each breeding season. About 45% of the nests were on electric power poles near farms and ranches. While recording the number of nestlings and their status, we noted that birds always incorporated twine in nests near agricultural fields, especially when nests were near fields of hay or herds of livestock such as llamas, horses, and cattle. The twine was a distinctive red-orange or black and we were certain that the ospreys had obtained it from nearby fields. We collected twine from bales, fields, and nests and the materials were identical. Furthermore, we saw ospreys carrying twine.

In at least 20 instances so much twine had been collected that streamers of the material hung from the nests. On 12 occasions (260 nests) we observed nestlings entangled in it. One nestling had a large ball of twine around one foot, which held the bird down so that it could not easily stand up. Its feeding appeared to be hindered and its siblings appeared to be at an advantage when parents brought food. We (CRB, LBB) were able to free this bird and it eventually fledged. PJH observed a nestling which had a thin piece of twine around its beak and foot so that it could not lift its head or eat. This bird also was freed and it ultimately fledged. In at least five other nests the entanglement resulted in mortality. Young would sometimes fall from nests where they would hang suspended by the twine and eventually die, if not rescued. Without the assistance of humans, mortality would have occurred in 4.6% (12/260) of the successful nests.

Ospreys opportunistically add materials to their nests. Bent (1937) documented more than 50 items other than normal nest materials. Included were nets, fishing line, and pieces of rope. In our study, ospreys typically built their nests of sticks and grasses, but added other materials, including pieces of paper and

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other roadside debris. The baling twine presented two particular problems. First, the cordage was designed to be resistant to damage from weather; old, discolored pieces remained so strong that they could not be broken by hand and therefore were dangerous to nestlings for some time. Second, the twine also accumulated and draped over the sides of nests, where it sometimes crossed power lines and caused power outages in the rain (J. Lane pers. comm.).

It is our belief that local farmers and ranchers should be alerted to this possibility and asked to be careful to collect used twine, or at least cut it into smaller pieces. Modern hay bales often are circular and more than 3 m in diameter. Pieces of twine cut at only one point on such bales are several meters in length. Shorter strands would be less dangerous and possibly less attractive to ospreys.

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Ornithological Literature

Edited by Sara R. Morris

THE PURPLE MARTIN. By Robin Doughty and Rob Fergus. Univ. of Texas Press, Austin. 2002: 128 pp., 16 color and 4 black-and-white figures including 4 maps, 6 tables. $19.95 (hardcover).—The Purple Martin (*Progne subis*) has the distinction of being both the largest swallow in the world and the only bird that has become almost completely dependent upon human-built nesting structures over a large portion of its range. This easy-to-read book is a popular account of martin biology, with a heavy emphasis on the art and lore of human interaction with the species. After a short introduction, the authors provide two brief chapters on taxonomy and range. The former gives an overview of all seven martin species of the Western Hemisphere, with comments on species relationships. The chapter on migration and range covers breeding sites and migration routes and timing for each of the currently recognized subspecies, although more detailed data on the winter grounds is held back until a later chapter.

There follow two longer chapters of a more "popular" nature: one on the history of the human-martin relationship and the other on some generalities of bird conservation as they apply to the species. The latter includes such varied subjects as the economic value of martins and martin-inspired literature. The next and largest chapter is probably the most valuable resource in the book. It consists of an overview of martin biology, from nest-building and caring of young, through fall migration and wintering ecology, to the return of scouts the following spring. It includes detailed tables of nesting development, predators and parasites, prey items, migration recoveries, and vocalizations. Also presented are discussions of foraging behavior and physiology, making this chapter essentially a miniature version of a species account from *The birds of North America* series.

The final two chapters return to the subject of martins in the realm of humanity. The first is devoted to an overview of the several organizations that are wholly or in part devoted to Purple Martin conservation, while the second discusses the constantly evolving tactics that "landlords" are using to promote the species. The latter is of greatest use to those who wish to attract their own colonies of these birds. The book ends with a list of additional references, thus making it a generally useful publication for anyone interested in Purple Martins, with an emphasis on those among us with a vested interest in maintaining populations of North America's largest swallow.—PAMELA D. HUNT.

HYBRID DUCKS: THE 5TH CONTRIBUTION TOWARDS AN INVENTORY. By Eric and Barry Gilham. Privately published by B. L. Gilham, 90 Church Rd., West Row, Bury St. Edmunds, Suffolk IP28 8PF, United Kingdom. 2002: 64 pp., 95 full color photographs. £17.00 + £2.50 postage and handling to North America.—The authors have produced their second compendium of hybrid waterfowl, supplementing their *Hybrid ducks* publication of 1996 and the Bulletin updates published in 1998, 1999, and 2000. To date, their checklist consists of 220 hybrid combinations believed to be first generation crosses. Five hybrids are described for the first time, while new facts are included for some of the other 215 hybrid combinations that were described previously. All of the color photographs are new and they depict 80 different hybrids, including some examples of eclipse plumages and backcrosses.

The accounts for most hybrid combinations tend to be very brief summaries of published and unpublished records, museum specimens, published and unpublished illustrations, similar forms, and references. Detailed descriptions for most of these hybrids are found in the earlier publications or the cited literature. More comprehensive descriptions are provided for the newly described combinations and for those hybrids with significant new sources

of information. While most of the hybrid accounts provide only the basic facts, the escapades of the Speckled Teal (*Anas flavirostris*) × Laysan Duck (*A. laysanensis*) adults read like an avian soap opera and provide a good understanding of how some of these unlikely hybrid combinations occur in captivity.

The photographs are the most fascinating contribution of this publication. They are of excellent quality, and range from routine hybrids such as American Wigeon (*A. americana*) × Eurasian Wigeon (*A. penelope*) to the strange offspring of a Tufted Duck (*Aythya fuligula*) × King Eider (*Somateria spectabilis*) pairing, and other equally unlikely combinations. There clearly are lessons in avian genetics to be learned from these photographs, especially when the species and gender of each parent are positively known.

This book is not a stand alone publication, and the complete set of two books and three bulletins are needed to fully appreciate the currently described variety of hybrid waterfowl. These publications would be of interest to the waterfowl enthusiast as well as to birdwatchers. The authors admit to having seen photographs taken in the wild of 20 additional hybrids, and not being able to identify even one of the parent species with any confidence. Bizarre hybrid waterfowl are not necessarily confined to aviary ponds, and the known hybrids depicted in these publications may prove to be helpful the next time some strange looking duck appears at the local lake.—BRUCE PETERJOHN.

A GUIDE TO THE BIRDING HOTSPOTS OF ISRAEL: INCLUDING A SYSTEMATIC CHECKLIST OF THE BIRDS OF ISRAEL. By Hadoram Shirihai, James P. Smith, Guy M. Kirwan, and Dan Alon. Israel Ornithological Center, Society for the Protection of Nature in Israel, Tel-Aviv. 2000: Vol. 1. Northern Guide, 115 pp., 63 color photographs, 15 maps; Vol. 2. Southern Guide, 165 pp., 84 color photographs, 19 maps. $25 per volume (paper).—It has been almost two years since this guide was published, and this time has not only allowed me to read it several times, but also to receive feedback from many a foreign tourist who has attempted to bird Israel with these guides as their "bibles of the Holy Land." Here I present not only the contents of the guide and their worth, but also the comments of these birdwatchers in an attempt to help future users in the field.

Israel is a very complicated country, in every possible sense. This also holds true for birding through Israel. One can travel from the extremely dry and hot deserts to snow-capped Mt. Hermon in six hours, and the checklist has more than 500 species that may be encountered along the way. This guide has tried to simplify the trip for the birder by splitting the major regions into birding hot spots and by concentrating mostly on only the "hottest" of them. Each volume begins with an introduction to the region addressed, briefly presents an overview of the habitats and climate, and includes a chapter on "timing your visit," wherein expected species highlights are given for each month of the year. The majority of the two volumes comprises the site guides. These include sub-sites, the key species that may be observed, and an itemized introduction that corresponds to a color-coded map of the site. A checklist for all of Israel is included at the end of each volume.

Both volumes are profusely illustrated with excellent color photographs. The authors must be commended for not only including top quality pictures of the birds to be seen but also the vistas and panoramas of the various regions and habitats that comprise this small country. An attempt has been made to have pictures of relevant species and regions accompany the site descriptions.

The reader must understand that not all the birding hot spots are presented; the sites included are only the ones selected by the authors and are best known to the general public. The most blatant exclusion, in my opinion, is the central part of the country, and the volumes do not include the Sharon Valley and the Jerusalem area in their accounts. This creates a gap wherein there is a guide to the northern quarter of the country and to the southern half, but nothing of the central quarter of the State of Israel. This region includes some areas of political unrest; it is the birders' decision as to whether they wish to visit the region. Also included are some sites which are not necessarily a national hot spot; they are

included because of the interest of one or more of the authors.

My biggest complaint about this guide is the maps. The maps are informative, plain, and easy to read; however, they are without scale, and are not drawn to scale. This often has resulted in visitors either over- or underestimating the distances to be traveled and the time to be allocated for their trips. I strongly recommend that visitors accompany the guide with a road map to fully understand their plans and orientation for any itinerary they put together. Those who wish to take extensive hikes also must equip themselves with topographic maps because the changes in landscape, especially in the deserts, can be dramatic and extreme. These are not necessarily stressed in the text, and are missing from many of the maps. I have heard of situations where hikers who had set out on a walk that they expected to be across a flat plain found themselves faced with a steep climb. Also, the security problems in Israel necessitate that visitors know how close they are to a problem area; only a more detailed map allows a better perspective of one's location within the country.

One of the major complaints of the visitors is that although many good suggestions pertaining to health and security are given in the text, they are not self-evident or stressed, and much of this advice is discovered only in retrospect. The authors would have done the birding community a service by concentrating in a highlighted box all of their practical advice and suggestions.

I also do not understand why the authors did not combine the two volumes into one large volume, as they did for the Hebrew version of this guide. This would have given the reader the complete scope of the country, and also would have been less expensive. Also missing are emergency telephone numbers or contacts—small things that can make all the difference when traveling in a strange country.

If you plan to visit Israel, are limited in time, and wish to maximize your birding experience, either one or both of the volumes that comprise this guide will be instructive. However, do not forget that more reliable maps must accompany you in the field. In any case, even though I have stressed the weak points in the two volumes to help future visitors, these very well presented volumes should grace the shelves of any international birder who travels to places of ornithological consequence.—REUVEN YOSEF.

ARAB FALCONRY: HISTORY OF A WAY OF LIFE. By Roger Upton. Hancock House, Surry, British Columbia, Canada. 2002: 224 pp., 225 color photographs, more than 80 line drawings. $70.00 (trade edition, ISBN 0-88839-492-6), $120.00 (patrons edition, ISBN 0-88839-504-3), $600.00 (limited edition, ISBN 0-88839-503-5, hard bound).—This is a large format (8.5 × 11-inch), extensively illustrated book that is devoted to presenting the reader with the personal perspective of the author's years of field experience with Arab falconers and their methods. I found the line drawings by Peter T. Upton very descriptive and, as a raptor researcher, instructive. They complement the text well and add a dimension to the book that I find missing in many descriptive books. The book has nine chapters, a glossary of some falconry related technical terms in English and Arabic, and a page of "further reading" wherein a list of the books published to date on the subject are given.

The author describes life in the hunting and trapping camps in Saudi Arabia, the Gulf States, Syria, and Pakistan. He has traveled the Middle East since the 1960s and experienced first hand the revolution in society and how modernization has affected ancient customs and practices, including falconry. The first chapter gives a short description of the history of falconry and its place in Arab society and beliefs, and the present situation. Chapter 2 is a very detailed and well illustrated description of the raptors used in falconry by the Arabs. Chapter 3 describes in detail many of the trapping techniques, and is accompanied by many line drawings. Chapter 4 presents the reader with a working knowledge of the accessories of the falconer, termed "furniture." Chapter 5 details the training techniques. Chapters 7 through 9 describe the various quarry that range from the desert hare (*Lepus arabicus*) to gazelles (*Gazella* spp.), with Chapter 8 focusing on the Houbara Bustard (*Chlamydotis undulata*). The final chapter

describes the techniques used in caring for the falcons after a day's hunt.

The author presents his knowledge in a very simple manner that can be understood by anyone, including those with no working knowledge of falconry or raptor biology. However, I also found this to be a disturbing feature of the book because learning the apparently simple techniques could encourage amateurs to try their hand at trapping raptors, with no professional intention or ability to handle the trapped hawks. In today's conservation conscience world, I am of the opinion that one has to think twice prior to making easily learned techniques accessible to the public. Another point of discomfort for me was the impersonal and detached tone of the author throughout the book, especially when endangered species are the quarry.

I found the book very interesting and also learned quite a few things from it. This is a good book for those interested in adventure, Arab folklore, and the exotic and heady world of falconry.—REUVEN YOSEF.

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PROCEEDINGS OF THE EIGHTY-THIRD ANNUAL MEETING

SARA R. MORRIS, SECRETARY

The eighty-third annual meeting of the Wilson Ornithological Society was held Thursday, 11 April, through Sunday, 14 April, 2002, in Fort Myers, Florida, in joint session with the Association of Field Ornithologists. The meeting was sponsored by Florida Gulf Coast University and Corkscrew Swamp Sanctuary; and Jerry Jackson chaired the local committee, which also included Laurel Chaplin, Bette Jackson, Brent Jackson, Matthew Jackson, and Dewey Robinson.

The Council met from 13:15 to 18:36 on Thursday, 11 April, in Classroom B of the Corkscrew Swamp Audubon Sanctuary headquarters. That evening there was a barbeque dinner for the conferees at Corkscrew headquarters. Following the dinner and some bird watching, Jerry Jackson, chair of the local committee and president of the Association of Field Ornithologists, welcomed guests and introduced Scott Sutcliffe, Associate Director of the Cornell Laboratory of Ornithology and vice-president of the Association of Field Ornithologists, who gave a multimedia historical perspective of bird watching titled "Birding in the 21st century: from guns to microchips."

The opening session convened at 08:34 in the Sprint Room of the Whitaker Center on the Florida Gulf Coast University campus. Jerry Jackson welcomed conferees on behalf of the university and the Association of Field Ornithologists, provided a brief history of the university, and gave conference announcements. He introduced Ted Davis, the president of the Wilson Ornithological Society, who thanked the hosts and local committee, announced the procedural change from two business meetings to one, and asked conferees to please read the report of the nominating committee prior to the business meeting. Doris Watt gave announcements related to the scientific program and introduced Edward H. Burtt, who introduced the sixth annual Margaret Morse Nice Plenary Lecture, "Population change in migratory birds: insights from long-term studies in breeding and wintering grounds," presented by Richard T. Holmes of Dartmouth College.

The scientific program included 33 contributed papers organized into six paper sessions, 10 papers in a symposium on Red-cockaded Woodpecker biology, and 25 contributed posters in addition to the Nice lecture. The committee on the scientific program was co-chaired by WOS Second Vice-President Doris Watt and Erica Dunn, AFO.

On Saturday morning, conferees enjoyed field trips to Corkscrew Swamp Sanctuary, Okaloacoochee Slough State Forest, Tiger Tail Beach, and Ding Darling National Wildlife Refuge, which were led by Jerry Jackson, Bette Jackson, and Laurel Chaplin. On Sunday, additional field trips, including Fakahatchee Strand, were scheduled.

A social hour preceded the annual banquet, a southern buffet served in the Sprint Room of the Whitaker Center. After the dinner, President Davis briefly addressed the conferees, thanked Jerry Jackson for hosting the meeting and Doris Watt and the Scientific Program Committee for a successful meeting, thanked retiring Members of Council for their service, and welcomed the new Members of Council. At this time the following awards and commendations were presented:

MARGARET MORSE NICE MEDAL
(for the WOS plenary lecture)

Richard T. Holmes, "Population change in migratory songbirds: insights from long-term studies in breeding and wintering grounds."

EDWARD'S PRIZE
(for the best major article in volume 113 of *The Wilson Bulletin*)

E. Hank Taliaferro, Richard T. Holmes, and Joel D. Blum, "Eggshell characteristics and calcium demands on a migratory songbird breeding in two New England forests" Wilson Bull. 113:94–100.

LOUIS AGASSIZ FUERTES AWARD

Elena Catherine Berg, University of California at Davis, "Reproductive cooperation and conflict in the White-throated Magpie-Jay."

GEORGE A. HALL/HAROLD F. MAYFIELD AWARD
(formerly the Margaret Morse Nice Award)

Graham G. Frye, "Natal latitudes, routes, and destinations of Northern Saw-Whet Owls (*Aegolius acadicus*) migrating through the Northern Rocky Mountains: Answers from banding and stable isotope geochemistry."

PAUL A. STEWART AWARDS

Sara Ann Kaiser, Michigan State University, "Effects of landscape configuration on the breeding productivity of Wood Thrush (*Hylocichla mustelina*)."

Liba Pejchar, University of California, Santa Cruz, "Habitat selection, source-sink dynamics, and conservation of the Akiapolaau (*Hemignathus munroi*)."

Daniel M. Scheiman, Purdue University, "Effects of field quality on dispersal rates of Bobolinks."

Ruth B. Smith, University of New Mexico, "Relating distance traveled to body condition and hematozoan infection of the Sharp-shinned Hawk (*Accipiter striatus*) during fall migration."

WILSON ORNITHOLOGICAL SOCIETY TRAVEL AWARDS

Marja H. Bakermans of Ohio State University, "Local and landscape effects on Acadian Flycatchers in central Ohio riparian forests."

Kathi L. Borgmann of Ohio State University, "Influence of landscape context on exotic shrub cover in riparian forests: implications for breeding birds."

Jason Bulluck of Appalachian State University, "The importance of southern Appalachian wetlands to breeding birds."

Damion E. Marx of Texas A&M University, "Summer prescribed fire effects on grassland birds wintering in Texas mid-coastal prairies."

ALEXANDER WILSON PRIZE

(for the best student paper)

Kathi L. Borgmann, "Influence of landscape context on exotic shrub cover in riparian forests: implications for breeding birds."

LYNDS JONES PRIZE

(for the best student poster)

Natalie Dubois, "Egg-tossing behavior, mate choice, and parental investment in the House Wren (*Troglodytes aedon*)."

Selection committee for the Nice Medal: John C. Kricher (Chair), Charles R. Blem, Edward H. Burtt, Jr., William E. Davis, Jr., and Doris Watt; for the Edwards Prize: John Smallwood (chair), Doris Watt, and Jessica R. Young; for the Fuertes, Hall/Mayfield, and Stewart Awards: James Sedgwick (chair) and Brett Peterson; for Wilson Ornithological Society Travel Awards: Doris Watt (chair); for the Wilson Prize: Leann Blem (chair), Charles Blem, Charles Brown, Dale Gawlik, Joe Grzybowski, John Kricher, Donald Kroodsma, Sara Morris, and John Smallwood; and for the Lynds Jones Prize: Leann Blem (chair), Mary Brown, Dick Conner, Dale Kennedy, Craig Rudolph, John Smallwood, and Doug White.

COMMENDATION

WHEREAS the Wilson Ornithological Society held its eighty-third meeting jointly with the eightieth meeting of the Association of Field Ornithologists in Fort Myers, Florida; and

RECOGNIZING that the Scientific Program Committee, of Alicia Craig, Ricky Dunn, Scott Sutcliffe, and Doris Watt, provided a diverse, informative, and entertaining program of oral and poster presentations, including a workshop on the Red-cockaded Woodpecker; and

RECOGNIZING the many efforts of Linda Minde and Diane Tessaglia-Hymes in a variety of logistical support roles including registration, preparation of the program and abstracts booklet, and other behind-the-scenes organizational tasks; and

RECOGNIZING that the Committee on Local Arrangements, chaired by Jerry Jackson and including Laurel Chaplin, Bette Jackson, Brent Jackson, Matthew Jackson, and Dewey Robinson, provided conference venues at Corkscrew Swamp Sanctuary and Florida Gulf Coast University that encouraged active participation in scientific sessions, offered relaxing atmospheres for interacting with colleagues and friends, and provided frequent avian distractions; and

RECOGNIZING the generosity of the Whitaker Foundation, which provided lunch on campus for the conferees and thus increased birding time; and

RECOGNIZING our field trip hosts and chauffeurs, Jerry Jackson, Bette Jackson, and Laurel Chaplin, who gave us great birding opportunities at some of the most highly acclaimed birding spots in North America and who capably arranged regular overflights of Swallow-tailed Kites throughout the meeting;

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society and the Association of Field Ornithologists commend the Scientific Program Committee, the Committee on Local Arrangements, and all others who helped to make this meeting in Fort Myers a great success, which will be long remembered.

The commendation was enthusiastically passed by acclamation. President Davis then announced that fifty years ago Allen Press began to publish *The Wilson Bulletin,* the first of hundreds of scientific journals now published by the press. In honor of this anniversary, Guy Dresser, president of Allen Press, presented a $10,000 donation to the Wilson Ornithological Society. After thanking Guy Dresser and Allen Press, President Davis gratefully acknowledged Tammy Reasoner for her work with Allen Press and with the Ornithological Societies of North America on behalf of the Society. He then recognized the contributions of all student presenters, all conferees, and everyone who made the meeting a success. On behalf of the Association of Field Ornithologists, Jerry Jackson expressed thanks to councilors, local helpers, and the College of Arts and Sciences and the food service of Florida Gulf Coast University. After the awarding of door prizes and the encouragement of "young people in the audience" to get involved with the societies, the meeting was adjourned at 20:11.

BUSINESS MEETING

The business meeting was called to order by President Davis at 16:46 on Friday, 12 April 2002, in the Sprint Room of the Whitaker Center at Florida Gulf

Coast University. President Davis recognized a quorum. Secretary Morris presented a synopsis of the 2002 Council meeting. She noted that as of 15 March Wilson membership was 2066, including 207 students, and that 632 libraries and institutions maintain subscriptions to *The Wilson Bulletin.* Volumes 1 to 111 of the *Wilson Bulletin* are in the process of being converted from print to electronic form, to be available for free and housed at the University of New Mexico. Volumes 112 (2000) and 113 (2001) are accessible on the BioOne website, which means that full text articles are available to subscribers to BioOne. The Council approved securing the Bentley Library at the University of Michigan as the archivist for the Wilson Ornithological Society. The Council reelected John Smallwood as editor of *The Wilson Bulletin.* Council is recommending the amendment of the Constitution and By-Laws of the Wilson Ornithological Society. The Council will continue to work on the amendments to the Constitution and By-Laws during the coming year and will circulate a copy of the suggested changes to the Wilson membership prior to next year's annual meeting.

Future meetings of the Wilson Ornithological Society have been planned for 19–23 March 2003 at Ohio Wesleyan University and for the spring 2004 at the new Laboratory of Ornithology at Cornell University. The WOS also will co-sponsor the NAOC meeting in New Orleans, Louisiana, during the last week of September, 2002, and will sponsor a teaching symposium on Tuesday, September 24.

The secretary then asked the assembled membership to stand in recognition of the following members who had died since the last Wilson meeting: James B. Cope (Richmond, IN), Don R. Eckelberry (Babylon, NY), Garrett Eddy (Seattle, WA), Linus C. Hoffmesiter (St. Louis, MO), John C. Jones (Bethesda, MD), Nedra K. Klein (Kirksville, MO), Dr. D. Frank McKinney (St. Paul, MN), A.W. Novitsky (Buffalo, NY), J.B. Owen (Knoxville, TN), Dr. David B. Peakall (London, United Kingdom), Dr. Olin Sewall Pettingill, Jr. (Bedford, TX), Dr. S. Dillon Ripley (Washington, DC), Chandler Robbins, II (Gloucester, MA), Steven M. Speich (Tucson, AZ), Myron T. Sturgeon (Plains, OH), and Katherine M. Wakelee (Ventura, CA).

The treasurer's report was presented by Martha Vaughan, who indicated that an audit of the Wilson accounts was completed this year and that the Society's investments are now healthy.

John Smallwood gave the editor's report.

Jerry Jackson, chair, presented the report of the nominating committee, which recommended the following slate of candidates: President, William E. Davis, Jr.; First Vice-President, Charles R. Blem; Second Vice-President, Doris J. Watt; Secretary, Sara R. Morris; Treasurer, Martha Vaughan; Editor, John A. Smallwood; and Members of Council for 2002–2005, R. Todd Engstrom and E. Dale Kennedy. President Davis thanked the nominating committee and asked for any nominations from the floor. Hearing none, he accepted a motion to close nominations by John Smallwood, seconded by Dick Conner. Chan Robbins moved that the Secretary cast a single ballot for the nominees. Glen Woolfenden seconded the motion, and Secretary Morris cast the ballot, electing the officers and council members.

Jed Burtt spoke briefly about the 2003 meeting at Ohio Wesleyan University. The schedule will include the Council meeting on Wednesday (19 March); the Nice lecture and Clark symposium, which will focus on the evolution of birds in the Galapagos, on Thursday (20 March); field trips on Friday (21 March); and paper sessions and the banquet on Saturday (22 March).

President Davis adjourned the meeting at 16:59 after a motion from Jed Burtt, which Dick Banks seconded.

REPORT OF THE TREASURER

The following report was amended to reflect the complete fiscal year ending June 30, 2002.

STATEMENT OF FINANCIAL POSITION

FISCAL YEAR ENDING JUNE 30, 2002

ASSETS

Current Cash Assets	
Cape Cod Bank & Trust—Checking Account	$ 27,121
Cape Cod Bank & Trust—Savings Account	50,961
Mellon Bank—Money Market Account	49,052
Dreyfus—Money Market Account	25,701
Comerica Checking—Van Tyne Account	1,670
First Source Bank Checking—Van Tyne Account	2,889
University of Michigan—Van Tyne Account	1,470

Total Current Cash Assets	$ 158,864
Investments (Unrestricted Fund and Sutton Fund)	
Mellon Bank—Government Obligations	$ 25,094
Mellon Bank—Common Stocks	760,717
Mellon Bank—Ltd Partnership	20,550
Total Investments	$ 806,360
TOTAL ASSETS	$ 965,225
FUND BALANCES	
Fund Balances—Beginning of Fiscal Year	$1,083,322
Current Year Change in Fund Balances	(118,097)
TOTAL FUND BALANCES—END OF FISCAL YEAR	$ 965,225

STATEMENT OF ACTIVITIES
FISCAL YEAR ENDING JUNE 30, 2002

REVENUE	
Direct Public Support (Contributions)	$ 11,727
Memberships & Subscriptions	55,661
Page Charges	6,635
Royalties	1,090
BioOne Electronic Licensing	6,859
Sale of Back Issues & Books (Van Tyne Library)	2,587
Interest Income—Cash Accounts	1,068
Investment Income—Dividends/Interest	21,273
Realized Gain (Loss) on Investments	(10,730)
Other Revenue	2,562
TOTAL REVENUE	$ 98,733
EXPENSES	
PROGRAM SERVICES	
Grants and Awards	$ 15,380
Van Tyne Library—Student Salaries & Benefits	2,059
Postage & Mailing	10,248
Printing & Editor's Costs	37,645
Electronic Conversion	24,243
OSNA Management Services	13,123
OSNA Executive Director	2,964
Award Costs	801
Support—Ornithological Council	3,000
Dues—American Bird Conservancy	150
TOTAL PROGRAM SERVICES (89%)	$ 109,614
SUPPORT SERVICES	
Audit & Tax Preparation Fees	$ 2,695
Office Supplies, Software, Postage	719
Storage Costs—Back Issues	511
Travel Expenses—Ornithological Council, OSNA, Annual Meetings	2,029
Insurance Expenses	1,805
Van Tyne Library Expenses	1,172
Investment Fees	3,330

Other Expenses	763
TOTAL SUPPORT SERVICES (11%)	$ 13,023
TOTAL EXPENSES	$ 122,638
EXCESS (DEFICIT) FOR THE YEAR—OPERATING	$ (23,904)
UNREALIZED GAIN (LOSS)—INVESTMENTS	(94,193)
TOTAL EXCESS (DEFICIT) FOR THE YEAR	$ (118,097)

Martha Vaughan, *Treasurer*

EDITOR'S REPORT—2001

A total of 175 manuscripts was received during 2001, which is about 19% fewer than the mean for the three-year period 1997–1999, but equal to the preceding 10-year mean. Most papers received three peer reviews (mean of 2.67). Of 465 copies sent for review, all to referees whom had accepted our invitation to review, nearly all (96.6%) were returned: 50% within 38 days and 90% within 62 days. The acceptance rate was 36%, a continuation of the increased selectivity of the *Bulletin* in recent years. Volume 113 consists of 42 major papers and 28 short communications. All four issues contain a color frontispiece, three of which are original paintings and one a series of illustrative photographs. The March issue included an additional color figure, and the December issue includes two additional papers with color figures.

The editorial office experienced a significant backlog during 2001, mostly attributable to two factors. The first was insufficient support due to a turnover in our undergraduate editorial assistants and a chronic breakdown of our e-mail; both of these problems have been corrected. The second factor was a temporary difficulty with the editor's schedule during spring. To help work through the backlog, a number of outstanding manuscripts were reviewed during fall by Clait Braun, Doris Watt, Charlie Blem, and Dick Conner, to whom I extend my appreciation. We currently are submitting the quarterly issues of the *Bulletin* to Allen Press at five- to eight-week intervals, which is rapidly bringing the production back to schedule. Members should receive the September 2002 issue during that month.

Clait Braun, Richard Conner, Kathleen Beal, and Karl Miller continued to serve on the editorial board during 2001; I thank them for the many reviews they provided, and to Kathy Beal for her expert review of statistical procedures in several papers, and for compiling the index. Editorial assistants Christine Bandstra, Rachel Bailen, Riitta Haroutunian, and Sophia Spadavecchia performed many of the functions of the editorial office, including receiving, acknowledging, and tracking manuscripts; contacting referees and, when necessary, reminding them to return their reviews; assembling files for my perusal; and numerous other essential operations. I am especially grateful to Doris Watt, who reviewed each accepted manuscript for content and format, and proofread all the galleys. Montclair State University and the Department of Biology and Molecular Biology have supported the editorial office in many ways.

John A. Smallwood, *Editor*

The reports of the standing committees are as follows:

REPORT OF THE MEMBERSHIP COMMITTEE

Current members of the WOS membership committee are Laurie Goodrich, Chair, Hawk Mountain (PA), Jim Ingold of Louisiana State University (LA), John Smallwood of Montclair State University (NJ).

Membership of Committee: We could use two additional active participants. Any suggestions on how we could gather new input are welcome. Daniel Ingold of Muskingum College resigned from the committee due to commitments.

The circulation of the poster has waned substantially. People seem less willing to take extra luggage to meetings. I had planned to take it to Raptor Research Foundation meeting in Manitoba in October, but after September 11th, the luggage inspection and special regulation of boxes for international travelers discouraged me from doing so. Things are clearer now, and in the future this will not be a big problem.

Brochures were taken and placed prominently at the American Ornithological Union meeting in Seattle, Washington (August 2001), and the Raptor Research Foundation meeting in Manitoba (October 2001), and the display was placed at the Pennsylvania Ornithological Society meeting in State College, (PA) May 2001.

During 2002, Jim Ingold sent invitations for membership and a brochure to all non-members that presented at the 2001 Wilson meeting.

The WOS President continues to send letters of welcome to new members and letters of thanks to members upgrading their membership. Labels are provided on a monthly basis from Allen Press. (Membership chair filled in on recent round of letters.)

The membership chair regularly receives inquiries from members regarding the journal and the status of

their membership. Most of these are received via e-mail. Rate of messages has increased with journal lateness. All messages are responded to with explanation and forwarded to Chris Cudebec, *Allen Press,* as he manages the WOS database. A few people have written to get a receipt for their payment, which Chris has provided.

Last but not least, I have not yet completed the new display for the Wilson Society. I was juggling working on my Ph.D. and my job last year. I intend to pursue this in the next few months. I apologize for the delays.

For anyone attending a professional meeting that could receive, set up, and tear down the WOS display, I will be happy to ship it to site location and have it shipped back to me at the end of meeting. Similarly, anyone needing brochures, please contact me.

Laurie J. Goodrich, *Chair*

REPORT OF THE JOSSELYN VAN TYNE MEMORIAL LIBRARY COMMITTEE

The following happened over the past calendar year with respect to the library:

Loans:

82 transactions to 46 members. Total number of items sent was 406: 56 books lent, and 350 articles photocopied. We continue to assist authors of *The Birds of North America* accounts by providing copies of articles. That project is slated to be completed in 2002. We also have been assisting the editors for *The Birds of Africa* and *The Handbook of the Birds of the World.*

The artist involved in paintings for the new edition of *The Grzimek Animal Life Encyclopedia* project also has been using the library heavily. The paintings will be incorporated into Animal Diversity Web project and may be viewed at http://animaldiversity.ummz.umich.edu/.

Acquisition of volumes:

- A total of 152 publications were received by exchange with 120 institutions.
- 30 titles were gifts from 26 organizations and 34 more obtained via 27 subscriptions.
- 424 items were donated by 12 members, friends, and libraries. These donations included 2 books, 392 journal issues, 26 reprints, 1 report, and 2 misc. items.
- Members, friends and libraries donating materials were: W. A. Carter; Charles Collins, Julie Craves, Doug Faulkner for the Rocky Mt. Bird Observatory, Karl Haller, Lloyd Kiff for The Peregrine Fund, Ted Miller, The Nebraska Ornithologists' Union, The Patuxent Library, Carol Ross, Cliff Shackleford, and E. O. Willis.
- New items purchased for $119.58 included 4 publications and 5 bird song tapes.

Dispersal of volumes:

- As part of our effort to decrease our stock of back issues of *Wilson Bulletin,* we sent out 797 old issues for only the cost of postage.
- We sold 42 duplicate books and 64 duplicate journal issues for $1,362.80.
- We donated surplus material to the following libraries: Society of Caribbean Ornithologists' Library: 1 book; Hungarian Institute of Ornithology Library: 53 journal issues; Michigan Technology University Library: 332 journal issues.

Accessibility on the Web:

- The web site (http://www.ummz.lsa.umich.edu/birds/wos.html) continues to be enhanced. Journals currently received are listed on the site as well as how to access the University of Michigan's on-line catalogue, which can be used to check holdings. We also have our books listed for sale, and duplicate journal issues available for sale/trade.

We still need to reduce our stock of back issues of *The Wilson Bulletin.* We would like to have help from the Council in identifying libraries, people, and institutions that could benefit from getting back issues.

Thanks to: Joann Constantinides, the secretary for the Bird Division in the Museum of Zoology, who handles many of the library requests, and especially James Fidler, who has sorted many boxes of donations, sent out hundreds of back issues of *The Wilson Bulletin,* copied many articles for members, and generally made the library run smoothly. Janet Hinshaw is the one who needs the most thanks, given that she makes sure everything, and I mean everything, runs smoothly.

Terry L. Root, *Chair*

REPORT OF THE UNDERGRADUATE OUTREACH COMMITTEE

The WOS Committee continues to maintain the *Guide to Graduate Programs in Ornithology* on the WOS web site. We solicited updates and additions over the summer and fall of 2001. These changes were implemented by Janet Hinshaw.

Herb Wilson, *Chair*

REPORT OF THE CONSERVATION COMMITTEE

The Conservation Committee of the WOS has been largely inactive during the past year. In part, the lack of activity was due to the perception by the Committee Chair of a lack of clear policy and direction within the Society with regard to conservation. Thus, the Conservation Committee seeks the guidance of Council in establishing policies that relate to the Society's interest in and support for matters of avian conservation biology.

At the Council Meeting held during the 2001 Arkansas meeting the Council granted the sum of $3,000 to Birder's Exchange, a program directed by Betty Petersen, which was shared by the Manomet Center for Conservation Sciences and the American Birding Association. Since then, Birder's Exchange has been contracted fully to the American Birding Association. The program continues to thrive, dispersing used optics and

other equipment to students and ornithological researchers throughout Latin America. The Chair has requested a report from Ms. Petersen as to how the contribution of the WOS was utilized. That report will be distributed at the annual Council Meeting.

The WOS could continue some measure of financial support for Birder's Exchange, but the Committee believes it wise to instead have a general discussion of what the charge to the Conservation Committee should be before the Committee recommends any form of financial commitment.

The WOS supports the Ornithological Council, but OC clearly is not a conservation organization. To whatever degree OC supports conservation arises as a byproduct of OC's various positions on matters it deems to be of scientific importance to ornithologists.

The WOS once routinely passed resolutions at its annual meeting. Many were focused on issues of conservation, but that activity has been abandoned at recent annual meetings and it is arguable as to whether or not it ever had any significant efficacy. The Committee does not recommend returning to resolutions as the primary means of expressing the Society's views on conservation matters.

Recently the editor of the *Journal of Field Ornithology* announced a policy change (*JFO* 73 [1], page 1) in which the journal will include papers with "some focus on conservation of birds." The reasoning for such a policy is sound. There is a large and increasing volume of good science directed toward issues surrounding conservation. Indeed, there are peer-reviewed journals dedicated entirely to the subject.

Given that *JFO* has embraced conservation within its publishing niche perhaps WOS should consider enhancing its activities in support of researchers working specifically on research pertaining to conservation of birds. The Society could create a new category of research grant that deals with this area. None of our current research grant categories is specific for avian conservation research. The Conservation Committee could assume responsibility for review of proposals.

There may be other avenues for WOS to demonstrate involvement with avian conservation and thus we seek Council's collective wisdom on what we believe is an area within the Society currently lacking sufficient definition.

John Kricher, *Chair*

The Committee on the Scientific Program, which included Doris Watt, Erica Dunn, Alicia Craig, and Scott Sutcliffe, presented the following program, assisted by session moderators Charles R. Blem, Edward H. Burtt, Peter C. Frederick, Joseph A. Grzybowski, Donald E. Kroodsma, and Chandler S. Robbins.

PAPER SESSIONS

C. S. Adkisson, Roanoke College, Salem, VA, "Behavioral ecology of Blue Jays in citrus groves."

R. A. Askins, Connecticut College, New London, CT, "Effect of forest fragmentation on bird communities in Japan."

M. Bakermans and A. Rodewald, School of Natural Resources, The Ohio State University, Columbus, OH, "Local and landscape effects on Acadian Flycatchers in central Ohio riparian forests."

C. R. Blem, L. B. Blem, and B. D. Greenawalt, Virginia Commonwealth University, Department of Biology, Richmond, VA, "Nestling Prothonotary Warblers: factors affecting recovery rates."

K. L. Borgmann and A. D. Rodewald, The Ohio State University, School of Natural Resources, Columbus, OH, "Influence of landscape context on exotic shrub cover in riparian forests: implications for breeding birds."

R. Bowman, Archbold Biological Station, Lake Placid, FL, D. L. Leonard, University of Florida, Gainesville, FL, and D. Swan, Florida Fish and Wildlife Conservation Commission, Gainesville, FL, "Partitioning causes of low fledgling production by Red-cockaded Woodpeckers in south-central Florida."

L. Brock, D. B. Burt, and D. W. Coble, Stephen F. Austin State University, Nacogdoches, TX, and R. N. Conner, Southern Research Station, Nacogdoches, TX, "Habitat variation and reproductive success in the Brown-headed Nuthatch."

J. Bulluck, Department of Biology, Appalachian State University, Boone, NC, "The importance of southern Appalachian wetlands to breeding birds."

D. B. Burt and P. Coulter, Stephen F. Austin State University, Nacogdoches, TX, and H.-W. Yuan and S.-F. Hung, National Taiwan University, Taipei, Taiwan, "Antipredator benefits of coloniality in Blue-tailed Bee-eaters."

E. H. Burtt, Jr., Ohio Wesleyan University, Delaware, OH, "Growth and dispersal of fledgling Barn Swallows during their first three weeks out of the nest."

T. Calvin, E. D. Kennedy, and D. W. White, Albion College, Albion, MI, "Songs used in mate communication in House Wrens."

R. N. Conner, D. Saenz, D. C. Rudolph, and R. R. Schaefer, Southern Research Station, Nacogdoches, TX, "*Phellinus pini* decay in Red-cockaded Woodpecker cavity trees."

P. Coulter and D. B. Burt, Stephen F. Austin State University, Nacogdoches TX, and H.-W. Yuan and W. Li-Ping National Taiwan University, Taipei, Taiwan, "Parental effort and fitness in Blue-tailed Bee-Eaters."

G. E. Crozier and D. E. Gawlik, Everglades Division, South Florida Water Management District, West Palm Beach, FL, "The use of decoys as a tool for attracting and trapping wading birds."

E. Dunn, Canadian Wildlife Service, Ottawa, ON, D. Hussell, Ministry of Natural Resources, Peterborough, ON, and K. Hobson and L. Wassenaar, Environment Canada, Saskatoon, SK, "Deuterium isotopes in feathers help identify natal areas of fall migrants."

R. T. Engstrom and W. E. Palmer, Tall Timbers Research Station, Tallahassee, FL, "Two species in one

ecosystem: management of Northern Bobwhite and Red-cockaded Woodpecker in the Red Hills."

P. C. Frederick and J. A. Heath, Department of Wildlife Ecology and Conservation, University of Florida, Gainesville FL, and R. Bennetts, USGS, Florida-Carribbean Science Center, Gainesville, FL, "Effect of asynchronous nesting on accuracy of "snapshot" counts of nesting colonial birds."

D. E. Gawlik and G. E. Crozier, Everglades Division, South Florida Water Management District, West Palm Beach, FL, "Wading bird nesting effort as an index of wetland ecosystem integrity."

D. Gemmill, Climate Prediction Center, National Oceanic and Atmospheric Administration, Washington, DC, "Climate resources for field ornithologists."

J. A. Grzybowski, S. Noble Oklahoma Museum of Natural History, Norman, OK, and University of Central Oklahoma, Edmond, OK, "Populations of Black-capped Vireos in Oklahoma: cases of management, extirpation, and recovery."

A. Gullen, J. M. Ichida, and E. H. Burtt, Jr., Ohio Wesleyan University, Delaware, OH, "Comparison of microbial communities on residential and migratory sparrows (Emberizidae) in Ohio."

J. A. Heath and P. C. Frederick, Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL, "White Ibis integument color changes during the breeding season: hormonal correlates and use in breeding stage classification model."

C. Hess, U.S. Forest Service, Apalachicola National Forest, Bristol, FL, "Effects of Red-cockaded Woodpecker translocations on a donor population."

W. M. Hochachka and S. Kelling, Laboratory of Ornithology, Cornell University, Ithaca, NY, "Climate change is more than global warming: snow cover and winter distributions of birds."

J. A. Jackson, Whitaker Center for Science, Mathematics, and Technology Education, Florida Gulf Coast University, Ft. Myers, FL, "Sidelights on the history of the Red-cockaded Woodpecker."

F. C. James and W. R. Tschinkel, Florida State University, Tallahassee, FL and P. F. Hendrix and R. L. Potter, University of Georgia, Athens, GA, "A large-scale experiment on the relationship between fire ecology in longleaf pine forests and the Red-cockaded Woodpecker."

E. D. Kennedy and D. W. White, Albion College, Albion, MI, "Variation in songs of House Wrens."

D. E. Kroodsma, University of Massachusetts, Amherst, MA, R. W. Woods, Devon, England, and E. A. Goodwin, University of Massachusetts, Amherst, MA, "Falkland Island Sedge Wrens imitate rather than improvise large song repertoires."

R. P. Larkin and R. H. Diehl, Illinois Natural History Survey, Champaign, IL, and J. E. Black, Brock University, St. Catherines, ON, "Dawn ascent and reorientation by migrants crossing the Great Lakes."

K. Z. Marsack, N. Sowa, and E. D. Kennedy, Albion College, Albion, MI, "Comparing methods of extracting DNA from feathers of nestling House Wrens (*Troglodytes aedon*)."

D. E. Marx and S. J. Hejl, Department of Wildlife and Fisheries, Texas A&M University, College Station, TX, "Summer prescribed fire effects on grassland birds wintering in Texas mid-coastal prairies."

J. R. McCormick, Stephen F. Austin State University, Nacogdoches, TX, R. N. Conner, Southern Research Station, Nacogdoches, TX, D. B. Burt, Stephen F. Austin State University, Nacogdoches, TX, and D. Saenz, Southern Research Station, Nacogdoches, TX, "Influence of habitat and number of nestlings on brood reduction in Red-cockaded Woodpeckers."

K. Mix, Texas A&M University-Kingsville, Caesar Kleberg Wildlife Research Institute, Kingsville, and the Welder Wildlife Foundation, Sinton, TX, and W. P. Kuvlesky, Jr., Texas A&M University-Kingsville and Caesar Kleberg Wildlife Research Institute, Kingsville, TX, "Effects of summer prescribed fires on taxa richness and abundance of avian and macroinvertebrate populations and associated vegetative changes."

T. O'Connell, R. Brooks, and J. Bishop, Pennsylvania State Cooperative Wetlands Center, University Park, PA, "The North American breeding bird survey as source data for assessments of ecological condition with the bird community index."

A. A. Radomski and D. Freeman, USDA, Agricultural Research Service, H. K. Dupree Stuttgart National Aquaculture Research Center, Stuttgart, AR, "Management techniques to minimize Double-crested Cormorant and other fish-eating birds at aquaculture facilities."

C. S. Robbins, B. Dowell, and J. Hines, Patuxent Wildlife Research Center, Laurel, MD, and A. Cerezo, FUNDAECO, Guatemala, "Longevity records and survival estimates of birds in a Guatemala rain forest."

D. C. Rudolph and R. N. Conner, Southern Research Station, Nacogdoches, TX, and J. R. Walters, Virginia Tech, Blacksburg, VA, "Red-cockaded Woodpecker recovery: an integrated strategy."

R. R. Schaefer, D. C. Rudolph, R. N. Conner, and D. Saenz, Southern Research Station, Nacogdoches, TX, "Effects of male helpers and intraspecific intruders on nestling provisioning in Red-cockaded Woodpeckers."

J. A. Sedgwick, Midcontinent Ecological Science Center, USGS, Fort Collins, CO, "Geographic variation in the song of the Willow Flycatcher."

J. D. Semones and P. Frederick, University of Florida, Gainesville, FL, "Consequences of nesting date on nesting success and juvenile survival in White Ibises."

P. Small, Florida Department of Environmental Protection, Okeechobee, FL, and R. Mulholland, Florida Department of Environmental Protection, Apopka, FL, "Florida Grasshopper Sparrows and the Florida Park Service, Okeechobee, Florida."

S. M. Smith, Mount Holyoke College, South Hadley,

MA, "Changing patterns in a chickadee population: a long-term study."

J. A. Spendelow, J. D. Nichols, and J. E. Hines, USGS Patuxent Wildlife Research Center, Laurel, MD, and J.-D. Lebreton and R. Pradel, CEFE/CNRS, Montpellier, France, "Modeling postfledging survival and age-specific breeding probabilities in species with delayed maturity: a case study of Roseate Terns at Falkner Island, Connecticut."

J. R. Walters, Virginia Tech, Blacksburg, VA, "Management strategies for Red-cockaded Woodpeckers derived from basic biology: tests at Camp Lejeune and Eglin Air Force Base."

POSTERS

R. C. Banks, USGS-PWRC, USNM, Washington, DC, "Evolution of a citation."

K. S. Berg, Department of Biological Sciences, Florida International University, Miami, FL, "Vocal learning and nestling nutrition: a test of the nutritional stress hypothesis."

T. Breiehagen, G. E. Woolfenden, and R. Bowman, Archbold Biological Station, Lake Placid, FL, "Ptilochronology, growth, and survival of fledgling Florida Scrub-Jays."

J. Cely and L. Glover, South Carolina Department of Natural Resources, Sandhills REC, Columbia, SC, "Hurricane effects on bottomland hardwood birds: the rise and fall of the Hooded Warbler."

P. A. Daniels, K. A. Battaglia, and S. R. Morris, Canisius College, Buffalo, NY, "Comparison of migration estimates obtained from Doppler radar and mist netting."

D. Doberne and B. Drummond, Colby College, Waterville, ME, "Common Redpoll behavior in the presence of a predator at the feeder."

B. Drummond and D. Doberne, Department of Biology, Colby College, Waterville, ME, "The effect of mirrors and decoys on feeding behavior of the Common Redpoll."

N. Dubois and T. Getty, W.K. Kellogg Biological Station, Michigan State University, Hickory Corners, MI, "Egg-tossing behavior, mate choice, and parental investment in the House Wren (*Troglodytes aedon*)."

E. Estey and S. Vayda, Colby College, Waterville, ME, "Foraging patterns in the Colby College Arboretum."

G. A. Jones, K. E. Sieving, and S. K. Jacobson. Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL, "An assessment of bird faunas utilizing conventional and organic farmlands of North-central Florida."

P. Kalenda and S. Morris, Canisius College, Buffalo, NY, "Factors affecting landings by hand-feeding birds at Tifft Nature Preserve."

A. M. Larracuente, E. M. Turner, D. A. Liebner, H. D. Sheets, and S. R. Morris, Canisius College, Buffalo, NY, "Effects of model choice and pooling on estimates of migratory stopover."

E. Leichty and J. W. Grier, North Dakota State University, Fargo, ND, "High nest predation and low nest parasitism for Golden-winged Warblers in a relatively pristine environment."

D. A. Liebner, A. M. Larracuente, E. M. Turner, S. R. Morris, and H. D. Sheets, Canisius College, Buffalo, NY, "Analytic and numeric estimates of bias in population parameter estimates produced by pooling of capture-recapture data."

M. Monroe and G. Ritchison, Eastern Kentucky University, Richmond, KY, "Breeding biology of Henslow's Sparrows on reclaimed surface mines in Kentucky."

J. J. Nocera and G. Forbes, New Brunswick Cooperative Fish & Wildlife Research Unit, University of New Brunswick, Fredericton, NB, and G. R. Milton, Nova Scotia Department of Natural Resources, Wildlife Division, Kentville, NS, "Habitat selection in grassland birds: a test of the importance of public information to ideal-free distribution."

S. Parke, Colby College, Waterville, ME, "Geographic variation in irruptive migration patterns in Common Redpolls (*Carduelis flammea*)."

A. A. Radomski and D. Freeman, USDA, Agricultural Research Service, H. K. Dupree Stuttgart National Aquaculture Research Center, Stuttgart, AR, "Monitoring Double-crested Cormorants in the catfish production areas of Arkansas: 1999–2002."

L. Robinson, Bainbridge Island, WA and M. Mahaffy, USFWS, Western Washington Office, Olympia, WA, "Pigeon Guillemot nest box project, Protection Island National Wildlife Refuge, 1994–2001."

H. Sofaer, Colby College, Waterville, ME, "Response of Black-capped Chickadee winter flocks to White-breasted Nuthatch vocalizations."

J. Speicher, Cresco, PA, J. Cherepko, East Stroudsburg, PA, and D. Speicher, Cresco, PA, "Pocono Avian Research Center, Inc: connecting avian and human populations."

J. A. Spendelow, USGS Patuxent Wildlife Research Center, Laurel, MD, Corey M. Grinnell, University of Massachusetts, Amherst, MA, and J. Michele Kuter, Connecticut Audubon Society, Fairfield, CT, "Initial responses of Roseate and Common Terns to revetment construction at Falkner Island, Connecticut."

E. M. Turner, D. A. Liebner, A. M. Larracuente, H. D. Sheets, and S. R. Morris, Canisius College, Buffalo, NY, "Comparison of three approaches to the quantification of migratory stopover."

J. E. Urbanic and T. E. Nupp, Arkansas Tech University, Russellville, AR, "Nest success related to colony characteristics of interior Least Terns on the Arkansas River, Arkansas."

S. Vayda and E. Estey, Colby College, Waterville, ME, "An analysis of foraging patterns in three species of woodpeckers in the Colby College Arboretum."

ATTENDANCE

The following is a partial list of attendees that includes people who preregistered for the meeting.

ARIZONA: *Sonoita,* Brenda Houser, Fred Houser; *Tucson,* Clait Braun, Ruth Russell, Steve Russell.
CONNECTICUT: *New London,* Karen Askins, Robert Askins.
COLORADO: *Fort Collins,* James Sedgwick.
FLORIDA: *Cape Coral,* Jon Greenlawn; *Englewood,* Anita Wilson, Richard Wilson; *Fort Myers,* Bette Jackson, Jerome Jackson; *Ft. Lauderdale,* June Ficker; *Gainesville,* Mary Clench, Peter Frederick, Gregory Jones; *Lake Placid,* Reed Bowman; *Miami,* Karl Berg; *Naples,* Terry Doyle; *Palm Beach Gardens,* Kathryn Smith, Rua Stob; *Tallahassee,* Michael Evans; *Venus,* Sonya LeClair, Annette Sauter, Christopher Valligny, Glen Woolfenden, Jan Woolfenden.
ILLINOIS: *Champaign,* Ronald Larkin.
INDIANA: *Carmel,* Alicia Craig; *Notre Dame,* Doris Watt.
KANSAS: *Lawrence,* Guy Dresser, Tammy Reasoner.
KENTUCKY: *Richmond,* Mark Bostrom, Michael Hodge, Gary Ritchison.
MAINE: *Waterville,* Deborah Doberne, Brie Drummond, Erin Estey, Susannah Parke, Serena Vayda, Herb Wilson.
MARYLAND: *Laurel,* Chandler Robbins, Diana Spendelow, Jeff Spendelow.
MASSACHUSETTS: *Amherst,* Don Kroodsma; *Chilmark,* Allan Keith; *Foxboro,* William Davis, Jr.; *Pocasset,* John Kricher, Martha Vaughan; *South Hadley,* Susan Smith; *South Natick,* Elissa Landre.
MICHIGAN: *Albion,* Tammy Calvin, Dale Kennedy, Kami Marsack, Nate Sowa, Douglas White; *Ann Arbor,* Janet Hinshaw; *Grand Rapids,* Peter Andree; *Hickory Corners,* Natalie Davis.
NEW HAMPSHIRE: *Hanover,* Richard Holmes.
NEW JERSEY: *Cape May,* Thomas Parsons; *Randolph,* John Smallwood, Mary Anne Smallwood, Nathan Smallwood.
NEW YORK: *Buffalo,* Katherine Battaglia, Peter Kalenda, David Liebner; *Fulton,* Erica Turner; *Grand Island,* Sara Morris; *Ithaca,* Linda Minde, Wes Hochachka, Scott Sutcliffe; *Lancaster,* Amanda Larracuente.
NORTH CAROLINA: *Boone,* Jason Bulluck; *Chapel Hill,* Helmut Mueller.
NORTH DAKOTA: *Fargo,* Ellen Leichty.
OHIO: *Columbus,* Marja Bakermans, Kathy Bormann; *Delaware,* Edward Burtt, Pam Y. Burtt, Amy Collins, Amy Gullen, Amy Schneider.
OKLAHOMA: *Norman,* Joe Grzybowski.
PENNSYLVANIA: *Allentown,* Daniel Klem; *Cresco,* Judy Cherepko, Darryl Speicher, Jackie Speicher; *Pittsburgh,* Ellen Parkes, Kenneth Parkes.
SOUTH CAROLINA: *Columbia,* John Cely.
TEXAS: *Nacogdoches,* Brent Burt, Priscilla Coulter, Richard Conner, D. Craig Rudolph, Daniel Saenz, Richard Schaefer.
VIRGINIA: *Alexandria,* Richard Banks, Betty Anne Schreiber; *Blacksburg,* Jeff Walters; *Front Royal,* Gene Morton; *Richmond,* Charles Blem, Leann Blem; *Salem,* Curtis Adkisson.
WASHINGTON: *Bainbridge Island,* Lee Robinson.
WASHINGTON, DC: Daphne Gemmill.
CANADA: *Fredericton, New Brunswick,* Joseph Nocera; *Ottawa, Ontario,* Erica Dunn.
NORWAY: Torgrim Breiehagen, Anne Mette Monclair.

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